

**Primate Social Cognition:
Group Responses to Specially Skilled
Individuals in a *Macaca fascicularis* Group**

INAUGURAL-DISSERTATION
zur Erlangung der philosophischen Doktorwürde
vorgelegt der Philosophischen Fakultät II
der Universität Zürich

von
Eduard Stammbach
von Zürich

Begutachtet von Herrn Prof. Dr. Hans Kummer

Zürich 1987
Zentralstelle der Studentenschaft

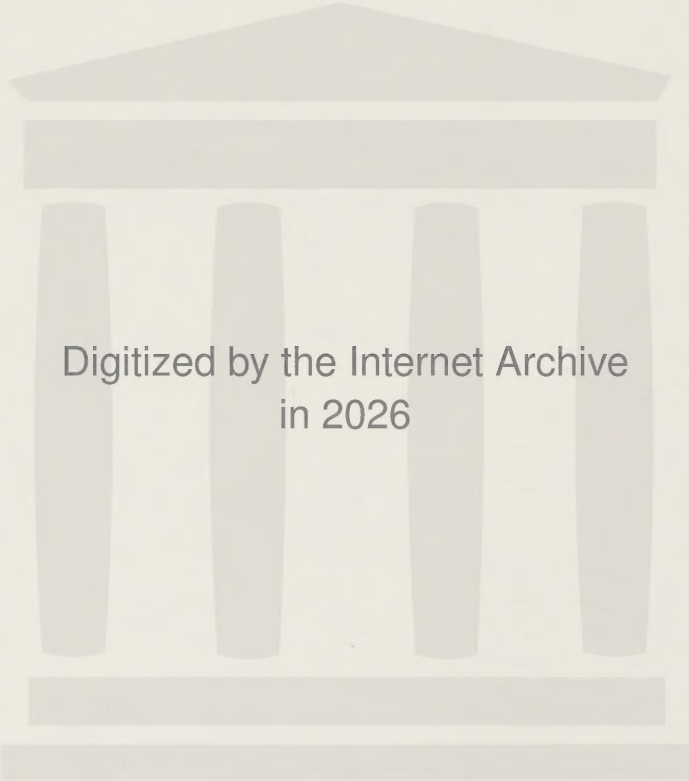
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Contents

Abstract	2
1. Introduction	3
1.1. Problem	3
1.2. Hypothesis and Predictions	6
2. Animals, Material and Methods	8
2.1. Animals, Subgroups	8
2.2. Experimental Design, Apparatus	9
2.3. Subgroups, Replicates	12
2.4. Data Registration and Analysis	12
3. Results	15
3.1. Qualitative Description of the Replicates	15
3.2. Dominance Structure	16
3.3. The Special Situation of the Subgroup	16
3.4. The Specialists' Activities	18
3.5. Lever Manipulations by Others	18
3.6. Feeding Partners Tolerated by the Specialist	19
3.7. Displacing and Chasing the Specialist	22
3.8. Following and Passing the Specialist	23
3.9. Significance of Food Site	26
3.10. Changes in Social Interactions	27
3.11. Duration of Knowledge	32
4. Discussion	34
5. Summary	41
6. References	43
7. Zusammenfassung	47
8. Ethogram	49
Tables and Figures	51

Abstract

This study is an experimental investigation of the competence of primates in appreciating the special skills of particular individuals in a group, and in modifying their behaviour accordingly. Eight low ranking individuals in a group of long-tailed macaques were trained as food-producing specialists at a lever-operated apparatus and subsequent changes were recorded in the interactions between these individuals and the other members of the group. It is shown that high ranking individuals, who at first chased the specialists away from the food-source, came to appreciate the benefits of holding back, thus gaining food provided by the specialist: but there was an element of trading also, for the specialists later gained more grooming from some of the dominant members. Just how fine the discrimination was which one individual makes about the characteristics of others was revealed by the way these grooming patterns were adjusted to experimentally controlled changes in the specialist skills of different individuals. The results are discussed in terms of cognitive abilities and reciprocal altruism hypotheses.

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1. Introduction

1.1. Problem

A great variety of methods are used to investigate the relation between primate social organization and ecology. These methods embrace gross correlational analyses of biological relevant variables at one extreme (Clutton-Brock & Harvey 1977) and detailed studies of individual learning capabilities at the other. One attempt to examine the relation between social behaviour and ecological performance is described by Jorde & Spuhler (1974). In a multivariate analysis of demographic, ecological and social variables taken from 21 primate species, they searched for clusters of variables such as day range, home range, arboreality, available food, group size, age-sex-class composition, aggressivity and type of social group. More intensive studies dealing with the adaptive values of primate social relationships have focused on the level of the entire group (e.g. Crook 1970, Kummer 1971, Altmann, S. 1974). A first attempt to consider the contributions of individuals to a social group was provided by Hinde (1974). He developed a conceptual order of social organization of primates, which involves three levels: (i) dyadic interactions among individuals which describe the momentary behaviour, (ii) long-term social relationships consisting of the pattern of a sequence of interactions and (iii) the social structure which is the result of the patterning of social relationships. Hinde's concept, however, does not take into account the interaction of a social group with its environment. Nagel (1979) developed a new tool for obtaining data relevant to the topic. According to his conceptualization one should identify types of dyadic interactions and relationships as basic units of the social system and ask in addition how the dyad handles an environmental problem in a social manner. The link between social organization and ecology is thus made on a very basic level. Kummer (1978), in an extension of Hinde's social and Nagel's socioecological approaches, assumes that an individual shapes its relationships in such a way that it increases his chances of reproduction. Kummer suggests that each conspecific B of an individual A can, in various ways, increase or

decrease the survival and thus the reproductive success of A. The effects of B on A depend (i) on B's qualities, on his skills, power and experience, (ii) on B's short- and long-term tendencies to perform acts that increase or decrease A's success in a given context and (iii) on B's availability. According to Kummer, the value of a partner may be increased by (i) monitoring the state of the three factors, (ii) by selecting the best and most available of the potential partners accordingly and (iii) by altering the states of the factors of the chosen partner. How this could be achieved is provided in an example of Seyfarth & Cheney (1984) who claim that grooming between individuals increases the probability that they will subsequently attend to each others' solicitations for aid. Kaplan (1978) as well found that individuals that groomed other individuals were more frequently joined in alliances by them. The best partner that an individual might choose among the members of a group would be a skillful, powerful and experienced partner that is likely and inclined to improve his success and that is not "occupied" by a dominant group member. A crucial point of the approach of Kummer is the necessity that monkeys should be able to evaluate their conspecifics.

Few studies have directly addressed a monkey's abilities to assess characteristics of others. Bachmann & Kummer (1980) showed that hamadryas baboon males (*Papio hamadryas*) were less likely to challenge the female in possession of another male when the female preferred her present owner as measured in choice trials. Hamadryas males thus seem to be capable of assessing social preferences of females; however, the experimental procedure did not exclude the possibility that the rivals read the relationship from the behaviour of only one dyad member. From a field study, Cheney & Seyfarth (1980) concluded that vervet monkeys (*Cercopithecus aethiops*) are able to perceive their group as structured into different social units. By replaying the screams of juveniles to their mothers, the authors showed that mothers respond to the scream replays by orienting towards the loud speaker with significantly shorter latency and longer duration than do non-mothers and playback increased the probability that controls looked at the mother. In a recent study that was carried out in our group Dasser (in press) was able to demonstrate that longtailed macaques (*Macaca fascicularis*) have the abil-

ity to express concepts of social relationships by their choices of slides of group members. In a discrimination test, one subject correctly identified 14 out of 14 mother-offspring pairs. Another animal correctly matched views of offspring to their mothers in 20 of 22 pairs in a matching to sample task. Both subjects apparently used a concept analogous to our mother-child-relationship.

In this study, I experimentally approach the ability of primates to monitor and use non-social skills of conspecifics. I do not attempt to identify the form of representation in which this knowledge about others is stored in the monkeys' brains. But the flexibility of behavioural reactions according to eventual changes of individual characteristics indicates at least the minimum cognitive performance that is needed for explaining the observed phenomena: The more a monkey is capable of judging characteristics and qualities of others, the more we will expect him to adjust his behaviour accurately and quickly in order to benefit optimally from the capabilities of his conspecifics.

I chose the following procedure: In a first phase, I ascertained that all group members were able to attain some of their food by manipulating a popcorn dispensing apparatus, thus introducing the knowledge that lever pulling can produce food rewards into a group of longtailed macaques (*Macaca fascicularis*). Then a single individual that, because of its low dominance status, could not monopolize the apparatus, was trained in a more complex manipulation task. This task consisted of manipulating three levers in a correct sequence, whereupon food became available for himself and other group members. This specialist thus became the only producer of preferred food in the group. The idea to use an operant learning task was suggested by Meier et al. (1968). The main questions of the study were:

- (i) Is it possible to establish low ranking animals as food producing specialists?
- (ii) Will other group members become aware of the special skills of that individual and will they adapt their behaviour accordingly in order to benefit from his skills?
- (iii) Will there be any effects upon the dominance or social relationships in the group? Thus, rather than using existing differences in skills, I analysed whether monkeys are able to assess differences in skills that are introduced experimentally.

1.2. Hypothesis and Predictions

I hypothesize that monkeys assess the skills of their group members and treat them so as to gain maximal benefit from them. Based on this hypothesis we can formulate the following predictions:

- 1) In course of the trials, the specialist should manipulate levers more and more exclusively. Non-specialists that all were trained previously to operate successfully the one-lever apparatus should reduce their own unrewarded manipulations of the three-lever apparatus, even though they observe that the specialist's manipulations are still rewarded.
- 2) High ranking group members should stop chasing the food producing specialist away from the preferred food site. Since there is no a priori reason to assume that a low ranking specialist will be allowed to monopolize the apparatus just due to his exceptional skills high ranking group members will at first try to get access to the food rewards and thus displace the specialist. Next, the specialist will hesitate to continue to manipulate levers and eventually other group members should hold back their challenges in order to keep the specialist "working" for them regularly.
- 3) Other group members should seek spatial proximity to the specialist as soon as he is approaching the food dispensing apparatus and try to join him so that they are present when the first food items are produced.
- 4) Following Kummer's (1978) hypothesis that animals may try to alter the tendency of others to improve their own success in a given situation, I expect that the food producer should be treated in a friendlier way than before. Interactions such as grooming should increase; aggressive acts should decrease. An increase should be observed in providing alliances. If we consider proxemics as a further measure of social attention, we expect group members that benefit from the specialist to maintain spatial proximity to him even outside the

experimental situation, thus indicating their closer association to the specialist as a consequence of the gained benefits.

- 5) We may even expect that food producers improve their dominance status. This would be the most extreme effect of the assessment of his skills by others.

2. Animals, Material and Methods

2.1. Animals, Subgroups

The study group consisted of 40 longtailed macaques (*Macaca fascicularis*) and was naturally composed. The animals stem from a large group from the Basle Zoo (Switzerland), where they had lived together since birth. They were separated from their native group and transferred to their new living quarters in summer 1981. Matrilineal kinship of the group is known. The group was permanently housed together in a 50 sqm indoor cage and a 1000 sqm outdoor enclosure and was fed three times per day with cereals, seasonal fruit and monkey pellets. Experimental animals were not deprived of food before experiments. Besides feeding times and during the night, the colony was allowed to interact freely for at least one and a half hour a day.

The experiments were carried out on subgroups of the colony. A subgroup was separated from the entire group for each experimental trial (p 10/11). In each of three consecutive years (1983/4, 1984/5, 1985/6) one of three different subgroups was used (Tab. I). The three subgroups were used in turn by three independent projects. No other projects were carried out simultaneously on one experimental subgroup. The subgroups consisted mainly of young males (subgroup 1), of young females (subgroup 2) and of adult females (subgroup 3), respectively. Mothers had their youngest offspring with them. Ketut was taken away from subgroup 1 for the last 20 trials as he was involved in severe rank competition fights in the colony. As a consequence he lost interest and stopped responding in the trials. As Tab. I shows, three females participated in two subgroups. Titin was a member of subgroup 1 as of subgroup 3. She had to be included in subgroup 1 since her son, Junus, was still dependent on her and could not be separated from her for trials. Topi and Sapi belonged both to subgroups 2 and 3. Topi, at first member of subgroup 3, was transferred to subgroup 2 in order to replace a young female that was not

available for this study. Sapi was taken away from subgroup 3 and was transferred to subgroup 2 as she reached subadulthood and was no more dependent on her mother Sakri.

2.2. Experimental Design, Apparatus

Apparatus

The apparatus consisted of two parts: (i) The three levers that had to be manipulated in a correct sequence in order to release a food reward. (ii) A food dispensing mechanism that provided preferred food in three bowls (Fig. 1). Three vertical levers 12 cm long were situated at a height that allowed a monkey to manipulate them in a sitting posture. Distance between levers was 12 cm. Even half year old infants could manipulate the levers without considerable effort. A lever had to be pulled to an angle of 45° to release the food dispensing mechanism. Thus the movements that had to be performed were clearly visible to other group members. A correct manipulation consisted of pulling first the left, then the central, then the right lever. Every 20 seconds, a monkey had 10 seconds to make a correct manipulation. During these 10 seconds, a beeper indicated that the levers were activated. For the whole period, when the apparatus was ready for manipulation, a yellow xenon light blinked. The three food bowls were installed beneath the levers, the middle one directly under the levers and the other two on the left and on the right at a distance of 50 cm. Thus, if a monkey manipulated the levers correctly, he himself and at least two other monkeys could eat from the food reward. One reward consisted of about a dozen fresh pieces of popcorn, a food cherished by the monkeys.

The apparatus and the electronic control were developed and built by the author. The food dispensing mechanism was based on an idea of Hachet (1974). Electronic circuits were developed by using TTL-components (Beckmann & Jeschke 1980, Beckmann & Jeschke 1981)

In summer, the trials were carried out in the larger part of the outdoor enclosure (Fig. 2). The rest of the colony had free access to the small enclosure and was visible to the experimental subgroup. In winter, the experiments took place in one half of the indoor cages (Fig. 3), while the rest of the group remained in the other half. Three of the replicates (p 12) were carried out partly in the outdoor and partly in the indoor enclosures. Changes from the outdoor to the indoor enclosure were necessary when the temperature sank below 5° C. Changes from the indoor to the outdoor enclosure were forced by the animals themselves since they refused to take part at indoor experiments when the sun was shining outside.

For the last five replicates (p 12) and thus for the last five specialists two apparatus were available. Alternately, only one of the two was switched on with a maximum interval of 5 min. This was done for two reasons. (i) In the first three replicates and especially at the beginning of a replicate, i.e. when a specialist had to get accustomed to his role, he often did not dare to approach the apparatus again after he had been chased away, since the chaser often remained near the apparatus. The availability of two apparatus sites improved the possibility to train and to establish the shyer female specialists. When a dominant group member occupied one apparatus, this was switched off and the other was switched on at the beginning of the following 20 sec interval. (ii) The manner with which other animals approached the apparatus relative to the position of the specialist could indicate whether they were aware of the skills of the specialist (p 23). By alternately switching on one of the apparatus the animals were forced to approach the newly activated apparatus several times per trial and thus more such data could be collected in the last five replicates. In contrast, insufficient data are available for the first three replicates.

Meteorological and organizational reasons did not allow application of exactly the same conditions for all trials. A single outdoor trial lasted one hour and a half. In the first 45 minutes (feeding phase), the apparatus was switched on, which was indicated by the xenon light blinking, and successful lever

manipulation was possible. In the second 45 minutes (social phase), the apparatus was switched off and social behaviour of the subgroup was observed. In winter, the social phase of the trials had to be reduced to 30 minutes for shortage of experimental time allotted to this study. Further reductions of the duration of single trials were necessary, since the colony was used by several experimenters. In trials 15-20 (p 8) of the first replicate and in trials 90-128 of the second replicate the social phase of the trials had to be left out completely. Differences in length of the trial phases will be taken into account when data are analysed statistically.

Training

Before the trials of the first replicate, each animal of the colony was pre-trained individually to manage a simpler task where only one lever had to be pulled twice consecutively to get a food reward. Thus, at the beginning of the experiments, all monkeys had experienced that lever pulling can produce a food reward. This training was repeated regularly for animals of the colony that did not belong to the subgroup that actually was involved in the experiment at that time.

The training of a specialist took place within the subgroup: The subgroup was released into the experimental enclosure but only the prospective specialist was now rewarded, at first for each single pull on one of the levers. Since the food reward could be suppressed by switching off the food dispensing part of the apparatus, no other subgroup member than the specialist himself could perform a rewarded lever manipulation. However, it was rarely necessary to switch off the food dispenser. In a next phase, not one but three levers had to be pulled, regardless in which sequence, to get a reward. Then, the specialist was gradually accustomed to pull the levers in a given sequence: In a first step, he had to pull the left lever once. Then he had to perform two pullings at one or both of the other levers. In the last step of training, he got the reward only if he pulled the correct sequence left → middle → right. The other subgroup members thus could observe how the specialist learned.

2.3. Subgroups, Replicates

On subgroups 1 and 2, three replicates with three different specialists were carried out in sequence, in subgroup 3 only two (Tab. II). Specialists were chosen by two criteria. They had to be as low ranking as possible (p 5) but nevertheless had to exhibit satisfactory lever pulling activity. The lowest ranking animals of the subgroups usually were too anxious to be trained as specialists. They hardly approached the apparatus in presence of other dominant group members. Before each new replicate, during which only the lever pulling of the specialist was rewarded, a preparatory series of trials took place, in which all the animals of the subgroup were allowed to manipulate one single lever successfully again. This phase served both to dismiss the previous specialist as well as to bring all subgroup members to lever pulling again. The previous specialist was not rewarded at all for the first three trials of this preparatory series. This phase lasted until every subgroup member had pulled levers successfully at least twice.

60 trials per specialist were planned, including the preparatory trials for all subgroup members. The schedule had to be corrected repeatedly and was applied for the first replicate only. The effective number of trials are shown in Tab. II. When the first two replicates with subgroup 1 were completed, it was apparent that up to 100 trials should have been carried out in order to fully produce the predicted effects. Unfortunately the specialists of three of the five remaining replicates ceased to pull levers before the planned number of trials could be carried out (p 15) and the replicates had to be terminated. The other three replicates had to be terminated when the subgroups were needed in other projects.

2.4. Data Registration and Analysis

During the feeding phase of a trial, protocols were spoken on a tape recorder and then registered on an electronic data collector

ZIRELCO-DATAPAD ®. I protocolled successful and unsuccessful lever manipulations by every individual using Hansen frequencies (Altmann, J. 1974). The 20 sec intervals were given by the apparatus. The detailed sequences in which the levers were touched was not recorded; it would have demanded most of the attention of the observer. Instead, social interactions (see Ethogram, p 49/50) among individuals were recorded. Duration of continuous behaviour was estimated by the scan sampling method (Altmann, J. 1974), using 20 sec intervals. At the end of each interval (scan sampling method) the locations of all animals were recorded, using a subdivision of the enclosure into three areas. This subdivision was different for outdoor and indoor trials (Fig. 2 and Fig. 3). In the outdoor enclosure, area 1, measuring 1 x 3 m, enclosed the part nearer than 1 m to one of the food bowls of the active apparatus. In the indoor cage area 1 measured only 1.7 x 1 m due to fixed cage structures. A second, larger area was situated around the food bowls at a distance from which the animals usually observed the behaviour of other group members at the apparatus. In the outdoor enclosure, area 2 extended 10 m from the food sites. Since enclosure posts served as reference marks, the border of area 2 and 3 was set at 10.8 m distance from the center food bowl (see Fig. 2). This distance was determined according to observations in the pilot experiments. In the indoor cage (Fig. 3), area 2 enclosed the cage where the apparatus was activated. Animals that stayed in area 3, which consisted of the rest of the enclosure or cage, did not seem to be interested in the experiment and usually were engaged in other activities. The importance of the differentiation between areas 2 and 3 will be explained on p 19, 22 and 24 (see also Ethogram).

Protocols of the social phase of a trial were typed directly into the data collector. I recorded all social interactions (see Ethogram) among individuals. Durations of continuous behaviours could be determined precisely by recording the start and the end of bouts. Every 5 min the nearest neighbour of each individual was recorded. If no animal was present within a 7.2 m circle of the focal animal no neighbour was protocolled. The 7.2 m distance corresponded

to the distance between enclosure posts. For each trial, the sequence in which the animals were selected was randomly determined.

Data were transferred to the IBM 3033 computer of the data processing center of the University of Zurich. Special programs for data processing were written by the author in FORTRAN-77 (SIEMENS 1983). In a first step data were tested for correct input codes and for correct registrations of behaviour durations. The program could detect the rare missing endings; the mistakes were inferred from the next entries on the respective individuals. This "debugging" program was used for durations of grooming. Statistical analysis was performed by using IMSL-Subroutines (IMSL Library, 1979) for the jackknife method according to Miller (Miller 1964, Mosteller & Tukey 1977, see also Bachmann & Kummer 1980) or by using the statistical analysis system SAS (SAS user's guide 1982 a and b) for Kendall rank correlations, Wilcoxon rank sum tests and iteration tests according to Shewart (Lienert, 1973). Graphs were obtained by using the SASGRAPH programming package (SASGRAPH user's guide 1985).

3. Results

3.1. Qualitative Description of the Replicates

Prediction 1 says that specialists should manipulate levers more and more exclusively in the course of the trials. Not all of the specialists acted with the same persistency. Remember that specialists were low ranking animals that could not monopolize food rewards simply due to their dominance status. They were often challenged by higher ranking group members, especially at the beginning of their careers.

The first juvenile male, Malen, was highly motivated for lever pulling and, towards the end of his replicate, he often stayed at the apparatus throughout a feeding phase. Malen hardly was displaced or threatened by other subgroup members. The other two juvenile male specialists, Ukui and Junus behaved similarly, but they were a bit more anxious than Malen. In contrast, three of the female specialists, Sakri, Sanah and Djambi ceased to operate the levers after a period of satisfactory activity. Sakri was challenged by Toko, one of the juvenile and high ranking males and gave up. Sanah was involved as a consort mate in male-male dominance fights in the colony and stopped her activity when she was slightly wounded. Djambi's replicate was started in the outdoor enclosure. When the trials had to be transferred to the indoor enclosure in autumn, the highest ranking group member, Rini, who had shown no interest in the apparatus up to then, displaced her consistently from the apparatus when she tried to approach. These replicates were terminated when the specialist refused to approach the apparatus for at least two subsequent trials. These last two trials were dropped from the data set. In the remaining two replicates with female specialists the latter overcame their initial shyness and showed satisfactory activity thereafter. Thus, five of the eight replicates led to satisfactory activities of the specialists.

3.2. Dominance Structure

In longtailed macaques the bared teeth grin is an unambiguous criterion of subordination (Angst 1974). In order to establish dominance orders in the three subgroups, I recorded all the bared teeth grins (all occurrences, Altmann, J. 1974) during both trial phases. Tab. III shows the resulting rank orders. The six dominance relations that were not defined by this criterion were determined by the approach-withdrawal behaviour of supplanting defined as follows: One individual approaches another one to a distance of 50 cm, the other withdraws within 2 seconds after the first has crossed the 50 cm line. The dominance order based on supplanting was exactly the same as found by the bared teeth grins. I therefore do not present the data.

No specialist changed his dominance position during his replicate. Thus, prediction 5 was rejected.

3.3. The Special Situation of the Subgroup

The trials were carried out in subgroups that were separated from the colony for the time of a trial. The question emerges whether the monkeys perceived the subgroup situation as something special or whether they behaved in the same way as in the colony situation. No differences in dominance order could be observed. In an attempt to determine whether partner preferences were also the same in the colony as in the subgroup, baseline data on nearest neighbours in the colony were collected in the same way as in subgroups. This was possible only in summer, i.e. when all the monkeys were in the outdoor enclosure. Once or twice a day the nearest neighbour of each of the individuals of the colony were recorded. Up to 40 neighbourhood scores for each subgroup member as a neighbour of one of the other subgroup members were collected.

I analysed the data as proposed by Stammbach & Kummer (1982). For each subgroup, dyads were ranked according to the neighbourship scores observed in the subgroups and in the colony and according to the grooming frequencies in the subgroups. These rankings of the dyads were compared with a Kendall τ correlation. In addition, a special method, called "Miller's jackknife" had to be applied, since there is no independence among dyads in which the same animal appears twice (see Mosteller & Tukey 1977, Bachmann & Kummer 1980). The jackknife method estimates the effect of independent individual components (in the present case of individual animals) by removing each of them in turn from the data. A correlation is judged to be significant if no significant influences of these individual components may be identified. The influences of individual components can be tested by using a t-test. The results are outlined in Tab. IV. Only subgroup 3 shows a significant correlation for all three comparisons, whereas in subgroup 1 and 2 only grooming frequencies as found in the subgroup condition are significantly correlated with neighbourship scores in subgroups. We thus have to conclude that the structuring of social relationships among the animals is not the same in the subgroups as in the colony, except in subgroup 3. Obviously the adult females showed their stable relationships regardless of the group situation, while the young males and the young females replaced some of their preferred partners that remained in the rest of the group and formed new preference structures in the subgroups. Qualitative impressions agree with these results. The animals seemed to be aware that they were separated just for the trials and some of them inactively waited to return to the other animals after the experiments. Therefore it would be questionable to search for experimental effects on the subgroup members when they lived in the colony. Of course, this will have consequences when discussing the results. If later analyses of data indicate experimentally induced changes in interactions among individuals, we should not refer to these changes as changes in long-term social relationships.

3.4. The Specialists' Activities

Fig. 4 shows the successful lever activities of the eight specialists, measured in numbers of 20 sec intervals with successful lever manipulations per hour (Hansen-frequencies, Altmann, J. 1974) The figures show that the three males, Malen (ML), Ukui (UK) and Junus (JN) and the two females, Saja (SJ) and Mayun (MY) pulled levers regularly and at quite a high frequency. A maximum of 180 lever manipulations per hour was possible. Females Sanah (SN), Djambi (DJ) and Sakri (SK), who "went on strike" before the end of the trial series as planned, had lower frequencies of manipulation. The most important precondition for successful completion of the experiments was fulfilled in five of the eight replicates: the subordinate specialists worked regularly in presence of other group members.

3.5. Lever Manipulations by Others

During trials in which a specialist was established, no other animal than the specialist himself was rewarded for lever pulling. At the beginning of a replicate, the other group members nevertheless continued to operate levers. According to prediction 1 (p 6), the other group members were to reduce their pulling of levers. Fig. 5 shows which proportion of lever pulling, successful and unsuccessful, was due to the specialist. All the eight graphs show the same tendency: While in the first trials of a specialist's series other individuals manipulated the levers too, the specialist performed almost 100% towards the end of the series. The three exceptions already mentioned, Sanah, Djambi and Sakri, had lower proportions throughout their trial series than the other specialists. All zero values indicate trials in which no lever pullings occurred at all.

3.6. Feeding Partners Tolerated by the Specialist

Measure of Benefit from Specialist

Before dealing with further predictions mentioned in the introductory section, we have to consider the way of measuring the amount of benefit that a group member gains from the specialist. At the end of each 20 sec interval I registered in which area of the enclosure each animal was staying, and thus could determine whether two animals were present simultaneously near the food bowls. If the lever was operated successfully food was present in the food bowls during that interval and the following one. Thus, the frequency with which an animal was present together with the specialist at the end of the interval when the lever pulling occurred or at the end of the following one, is a rough measure for the benefit that an animal gains from the specialist. These frequencies will be called frequencies of joint presence. As the first trials showed, it was unnecessary to distinguish whether an animal sitting in front of a filled food bowl was eating or not. I rarely saw a monkey that was not eating from the food except when his cheek pouches were already filled with popcorn. One might object that a simpler measure would have been more accurate in measuring the amount of benefit, namely the total number of intervals when an animal was present alone as well as together with the specialist at the food site when food was available. But I chose the joint presence version that takes into account the simultaneous presence of the specialist because the measure has to reflect not the total quantity of food that is gathered by an animal but the quantity of food that a non-specialist gathered after having observed the specialist's manipulations. If an animal arrived at the food site after the specialist already had left it is less likely that he noticed that the specialist was responsible for the food now available. The opposite is most likely true if the specialist remains at the food site after having manipulated the levers. The joint presence measure thus estimates the benefit as perceived by the non-specialists. Since the durations of the feeding phases of the trials were not equal within each replicate, the frequencies of joint presence were corrected for a standard duration of 60 min for data analyses across trials.

Closest Associations

Tab. V contains two scores that illustrate the different amounts of benefit gained by group members from the specialist. The first score ("trials together") indicates in how many of the trials of a replicate a group member was present together with the specialist in one interval or more per trial and thus represents the regularity of access in the course of a replicate. The second score ("intervals together") shows in how many of the total number of intervals per replicate in which food was provided a group member was present at the food site together with the specialist. This score estimates the amount of food that was gained in presence of the specialist throughout a replicate. In the following I will refer to this %-score as sum of joint presence. The dyads in Tab. V are arranged according to their sums of joint presence. Most replicates suggest a bimodal distribution of scores, which means that some of the group members had regular and frequent access to food, while others seemed to be excluded. Both measures reveal almost the same rank order of benefit gained by the non-specialists. The exclusion of some non-specialists may be due to two reasons. Either they were not tolerated by the specialist in that he left the food site when they approached, or they were displaced by higher ranking group members that themselves competed for maximal benefit with them. In the following I will not distinguish these two possibilities since (i) the aim of the study is to find out how an animal treats another one that benefits him with food and (ii) a detailed analysis of this question would be subject to additional experiments that would have demanded the removal of high ranking animals from the group in order to allow low ranking group members to approach the food site.

An arbitrary limit of 5% of the sum of joint presence divides the dyads into 17 (27%) high and 38 low profiteers. 36.1% of the non-specialists that were higher ranking than the specialist reached the high criterion, in contrast to only 21.9% of the lower ranking ones. Obviously, dominant monkeys tolerated a subordinate preferably if he was the profitable specialist. Across sub-

groups, the male specialists, Malen, Junus and Ukui, tolerated more other profiteers near them than did the female specialists, and the sum of joint presence scores calculated over one replicate tends to be higher in male specialists than in female specialists. Further data evaluations will determine whether this benefitting has consequences on interactions among specialists and non-specialists.

Variability of joint presence in course of a replicate

One could hypothesize that the amount of benefit that a non-specialist may gain from a specialist depends on a constant quality of the individual dyad. If so, a non-specialist should benefit about equally from a particular specialist throughout a replicate. I performed iteration tests according to She-wart (Lienert 1973, pp 479-481). This procedure looks for monotonous trends, either increases or decreases, in the data. The joint presence scores were pooled for each block of five successive trials in order to avoid too many zero scores that would have made the analysis impossible. Building blocks of five trials additionally results in reducing random oscillations due to short-term effects in single trials. For each specialist - non-specialist dyad the median of the joint presence scores over the blocks of five trials was calculated first. Then, the iteration test checked whether the observed scores of a replicate oscillate randomly in reference to their median or whether the scores of subsequent trials are located mainly above or below the median and thus formed clusters that would indicate systematic modifications of joint presence in course of a replicate. In nearly all the dyadic relationships monotonous modifications of this kind occurred in joint presence scores (level of significance $\leq 5\%$), with the exception of two mother-infant relations (Sanah-Saja and Sakri-Sapi) and the closest male-male relationship as judged on the basis of grooming (Ukui-Junus). The three relations share one common quality, namely high intimacy in terms of frequent spatial proximity and intense grooming interactions. All three dyads rank at the top in the respective scores of data in their subgroups. Perhaps these relationships already were at their optimal capacity of collaboration.

3.7. Displacing and Chasing the Specialist

The highest ranking group members usually try to monopolize the source if a limited source of preferred food is available in a monkey group. This happened in these experiments too, at least in the first trials of a replicate. As soon as a specialist operated the levers correctly, a high ranking group member approached and displaced or chased him away from the apparatus. Of course, no further food reward was available until the specialist returned to the apparatus and pulled the levers again. Prediction 2 was that the high ranking animals learned to approach cautiously and not to chase the specialist. However, not all the dominant non-specialists initially displaced and chased the specialist.

To test this hypothesis, I determined for each trial (i) in how many 20 sec intervals the specialist left the 1 m area around the apparatus; this number gives an estimated maximum number of intervals, in which the specialist could have left the apparatus because he was displaced or chased. (ii) How many of the leavings were preceded by displacements or chases? A leaving could be preceded by one or several displacements or chases performed by one or several group members. A displacement was protocolled when another animal entered the 1 m area situated around the apparatus and the specialist left within 2 sec afterwards. Chasing was recorded when the specialist was threatened or chased (see Ethogram) by others while he stayed in the nearest zone around the apparatus and left it within 2 sec.

The first question is whether the proportions of leavings due to displacements or chases were reduced in the course of the replicates, regardless of which animals were responsible. Tab. VI contains the Kendall τ for the correlation between the proportion of leavings induced by displacement or chasing in a trial and the ordinal number of the trials. In case of reduction of the proportion across subsequent trials, a negative correlation should appear. All τ s are negative, but only two are significant for displacing and six for chasing.

Thus, pooling the displacements by different actors does not yield as a clear reduction of displacement in the majority of specialists as it does for chasing. The same analysis was therefore carried out on the level of individuals (Tab. VII). Cases in which more than one group member displaced or chased the specialist were scored for each of them. In 14 of 55 dyads displacings were significantly reduced in course of the replicates. In only one the actor was lower ranking than the specialist. Chasing was reduced in 15 dyads of the 36 in which the specialist was lower ranking (= 41.6%). These higher ranking animals followed prediction 2 (p 6) of the project and thus realized one condition of profiting.

These findings give a first hint that some of the group members became aware of the role of the food producer and were able to hold back their chasing. This may be illustrated by a scene observed in trial 108 with Ukui as a specialist. Ukui calmly manipulated the levers and Ketut, the highest ranking subgroup member, sat near him and ate from the popcorn. As Junus approached, Ketut chased him violently, passing behind Ukui's back by some 10 to 20 cm only. Ukui did not respond to the chase as if he knew that it was not directed at him.

3.8. Following and Passing the Specialist

For the last five replicates two apparatus were available. Alternately, only one of the two was switched on. Thus, both specialists and non-specialists had to move from one apparatus to the other several times. How a non-specialist reacts to the movements of the specialist may give a hint on what he already knows about the specialist's role. An ignorant non-specialist should approach the apparatus only after a successful lever manipulation by the specialist, responding to the visible food only. Informed monkeys should approach the apparatus already when the specialist starts to approach it, they should follow or even pass him. Three stages of the learning process can be distinguished: (i) Another animal approaches after the specialist already manipu-

lated the levers successfully. (ii) Other animals follow the specialist while he approaches the apparatus in order to pull levers or (iii) they even pass and arrive before him at the apparatus, and wait for his lever pulling.

I defined two measures that reflect these patterns of behaviour. If the specialist approached the apparatus, which means that he walked or ran at least 1 m in the direction of the active apparatus while he was within area 2 of the enclosure, (i) following was protocolled if a non-specialist moved behind the specialist and in the same direction for at least 1 m within area 2 of the enclosure before the specialist entered area 1. (ii) Passing was recorded if a non-specialist after having followed arrived first at the food site before the approaching specialist. Passing was protocolled even if the specialist immediately left the apparatus again. The frequencies of both types of behaviour were divided by the total number of approaches to the apparatus performed by the specialist. If an animal learned about the skills of the specialist, both proportions should increase in course of the trial series. Passing was rare in the much smaller indoor cage and insufficient data are available on indoor trials (specialists Saja and Mayun). Unfortunately the replicates with low lever activity by specialists (Sanah, Djambi and Sakri) took place in the outdoor enclosure.

Within each specialist's trial series I looked for positive correlations (Kendall's τ) among the proportions and the trial numbers. Tab. VIII shows that in 7 dyads we can find significant positive correlations for following and in 4 dyads for passing of a total of 37 dyads that could be tested. No significant negative correlations are found. Of course we can not conclude from a non significant correlation that the respective dyad partner of the specialist was unable to assess the specialist's skills. He may have been prevented from following and passing by a higher ranking group member that had priority of access to the food bowls. The significant correlations are found in dyads with high sums of joint presences in which non-specialist partners had frequent access to the apparatus site and thus frequent opportunity to follow or pass.

We may conclude that some of the animals not only were able to perform the more simpler task of holding back their aggressive tendencies in order to get an increasing amount of benefit from the specialist, but that there was also an element of anticipation. Some animals obviously could associate the approaching of the apparatus by the specialist with the later provisioning of the food reward from which they could participate.

The following objection may be made: As mentioned earlier, a flashing light and a beeper indicated the activation of an apparatus. Thus the animals might have approached an apparatus merely reacting to these signals, and the following or passing occurred just because of the simultaneous approach of both the specialist and his partner towards a newly activated apparatus. This objection can be rejected though. When the alternative apparatus was switched on the specialists seldom approached it immediately. In at most 4 % of the cases they arrived at the apparatus site in the first 20 sec interval after the alternative apparatus was switched on. In about one third of the cases, the specialists arrived in the second interval. The peak for non-specialists appears in the third or in the fourth interval after the alternate apparatus was switched on. Therefore followings and passings of others really were reactions to the movements of the specialist. Furthermore, followings and passings were set into relation with the total number of approaches performed by the specialist and the changes of these proportions were analysed. Since due to the previous training procedure all the animals were very familiar with the apparatus it is improbable that these improvements of following or even passing were due to improved learning of the flashing light as a conditioned stimulus. We have to conclude that the animals learned that both conditions for food delivery had to be fulfilled, namely that (i) the apparatus had to be switched on and (ii) the actual specialist had to be present at the apparatus.

An impressive qualitative observation may illustrate that following and passing in fact indicate awareness of the specialist's abilities. In trial 369 with Mayun as specialist, she was slowly approaching the apparatus after having

hesitated for a couple of minutes. Djalan who at the time was digging in the soil 30 m away at once ran over, passed Mayun, sat near the apparatus and waited for her to operate the levers.

3.9. Significance of Food Site

The following finding was a surprise to me; therefore data collection and experimental design were not adjusted to this question. When I performed the basic training of all the monkeys of the colony in pulling one single lever I found no indication that a monkey that had learned the task in the indoor cage had any difficulty to remember the correct form of manipulation in the outdoor enclosure, and vice versa. But when the trials with Ukui as specialist were transferred from outdoors to indoors, observations suggested that the site where a specialist was trained influenced whether he was respected as a specialist at the other site. The question arose as to whether the animals generalize the skill of the specialists to many locations. Three of the eight replicates were transferred from indoors to outdoors or vice versa: Ukui, Junus and Mayun. They were fully accepted by the other group members as specialists when some of the following trials had to be carried out in the other enclosure because the weather changed. I compare the last three trials at the original site with the first three trials at the new one. As shown in Fig. 6 all three specialists manipulated the levers almost exclusively at the original site. But after the change of enclosure, the exclusivity of lever pulling dropped in all three specialists and other animals tried to get a food reward on their own. These results are significant for both Junus and Mayun (Wilcoxon rank sum test, $P \leq 0.05$) but not for Ukui. A fourth specialist, Djambi, even stopped operating levers in the indoor cage altogether. This, however, could be explained by the much smaller dimension of the enclosure.

These findings suggest that the "knowledge" of the specialist himself, and of others about his role is at first connected with the site where the specialist performs his activities and thus not a knowledge on his general abilities.

Nevertheless, Fig. 6 suggests that they quickly learn that the site of performance of the specialist is of inferior importance. The change in Ukui's replicate is probably not significant because the other animals learned too quickly that his special position was valid in the indoor cage too.

This finding will have consequences for the interpretation of the results. If the site where the specialist was trained influences the knowledge of his skills, it is also possible that the social environment, subgroup or colony, will have its effects as well and thus we may expect that a specialist that was trained in the subgroup is not regarded as a specialist in the colony by his subgroup members. Interpretation of data should therefore be regarded as valid for the subgroup conditions only.

3.10. Changes in Social Interactions

Until now I have described changes in the behaviour of the specialists and their partners while the apparatus was active. It should be easy for a monkey to learn to behave accurately in order to benefit from the food rewards that are provided by the specialist as suggested by prediction 2 and 3. The less he chases or displaces a specialist and the sooner he approaches the apparatus with the lever pulling specialist, the larger food reward he obtains. It would be less easy to explain if animals began to treat a specialist differently in the course of trials even at times when no immediate increase of a food reward results from their action. In order to test this, the trials were carried out in two phases. In the food phase of a trial the apparatus was switched on and the specialist usually manipulated the levers. In the subsequent social phase of each trial, the apparatus was out of action and thus no immediate food reward could reinforce changes of behaviour. Thus, we now turn to predictions 4 and 5 (p 6).

The dominance status (prediction 5) of the specialist was not affected (p 16). During the social phase, measures of social relationships were recorded,

namely (i) the spatial proximity of the animals serving as a measure of association among individuals and (ii) interaction data like grooming behaviour directed towards the social partner, aggressive behaviour and forming alliances in aggressive episodes. Since frequencies of giving alliances were very low, actor and receptor alliances (de Waal 1977) were not distinguished in this study.

During the social phases the nearest neighbour of each animal of the subgroup was protocolled every five minutes. The exact duration of each grooming bout was recorded. For aggressive behaviour and alliances the exact frequencies are available. Since the duration of the trials and trial phases were not equal for every replicate, the scores and durations were converted to rates and proportions per hour, respectively, for each trial.

A sufficient degree of certainty about experimentally induced increases or decreases of neighbourhood scores and behaviour scores requires three conditions in a specialist - non-specialist dyad:

(i) The group member must indeed have gained a satisfactory amount of benefit from the specialist. We can expect that animals that reached the highest scores on sums of joint presence should most likely change their behaviour directed towards the specialist as a reaction to the obtained benefits.

(ii) The changes in social measures should coincide in time with the experimentally determined specialization of individuals. For this purpose, I performed a first analysis using a Wilcoxon rank sum test for each of the 55 specialist-non-specialist dyads. I compared the neighbourhood scores and behaviour frequencies in the social phase of all trials during which the dyad member referred to as the specialist was indeed established as specialist (specialist trials) with the scores and frequencies of all trials when a third individual was the specialist (control trials). This analysis considers changes that are correlated with the experimental conditions that were set by the experi-

menter, i.e. which one of the animals is allowed to perform successful lever manipulations, and thus does not take into account the actual activity and eventual benefits from the specialists. It will locate significant influences of experimental conditions regardless of whether they are true dyadic effects among the specialist and a group member or complex triadic effects of the experimental condition. The Wilcoxon rank sum analysis thus is expected to reveal experimentally induced effects in dyads that do not correspond to our hypothesis. Therefore, we also should attempt to assess which of these significant effects can be attributed to mainly dyadic effects and try to exclude those affected by triadic processes. This will be done by the next procedure.

(iii) The changes of social measures should correlate with the amount of benefit gained per trial due to the specialist. For this second analysis, all specialist and control trials of a dyad were pooled. A Kendall τ correlation across trials per dyad between grooming and neighbourhood on one hand and joint presence on the other was calculated. Joint presence was zero by definition during the control trials, since the measure represents the amount of benefit gained from the specialist. Frequencies of sitting together at the food site without taking into account who operated the levers, however, would measure the mutual tolerance of two dyad members, strongly influenced by triadic effects. Furthermore, the analysis of displacing/chasing and of following/passing already suggested that non-specialists are aware that the specialist is associated with food production. I believe it is justified to assume that a non-specialist is aware that the lever manipulating specialist is responsible for food production and that merely sitting together at the food site is an unnecessarily crude criterion to estimate the gained benefit from the specialist. The Kendall τ measures the synchrony in the development of grooming and neighbourship and of profitable joint presence. It is not sensitive to delayed effects of profiting on the affiliation measures but in contrast to the Wilcoxon tests avoids false conclusions based on triadic effects. Thus, each statistical procedure has its weakness, which is why both are performed.

Before dealing with the results of the analyses, I would like to stress that the aim of this part of the analysis is not to detect all possible changes in social behaviour that might have been caused by the experimentally induced specialization, but to denote only the changes that are most probably due to experimental conditions. Tab. IX summarizes the results for neighbourhood scores and grooming frequencies. For each dyad the grooming given to the specialist as well as the grooming received from the specialist are analysed. The Wilcoxon rank sum tests reveal that, in 14 dyads, neighbourhood scores were significantly higher during the specialist trials and significantly lower in 8 dyads. In 13 of the relationships even the amount of grooming given to the specialist by the non-specialist was higher. Grooming was lower in 2 of the dyads. Systematic changes in grooming by the specialist occurred in 9 dyads: grooming was higher in 4 but lower in 5 dyads. For threatening, chasing and providing alliances it appears that for most of the dyads an insufficient amount of data was available. No significant reductions of threatening or chasing could be found. Concerning alliances a significant effect could be found in only one of the dyads: Djalan increased the number of alliances that he gave to Mayun (Wilcoxon rank sum test, $P \leq 0.05$). This case is attributable to chance. Significant positive Kendall τ correlations between joint presence and neighbourhood scores were found in 11 dyads, negative ones in 3 dyads. Correlations between joint presence and grooming given to the specialist are significantly positive in 12 dyads and significantly negative in 1 dyad. Correlations between joint presence and grooming received from the specialist are significantly positive in 3 dyads and significantly negative in 2 dyads. No Kendall τ correlations were calculated for the remaining measures, since the Wilcoxon rank sum tests had already shown that data are insufficient.

One might object that the change of intimacy as measured by neighbourhoods and grooming is not due to the specialist providing food, but simply due to the specialist sitting close to the feeding tray whenever the subject eats. This could be tested by comparing correlations between joint presence and grooming in the specialist and the control trials separately. If the correlations

held only for the specialist phase, one could conclude that the non-specialist increases his social attention to the specialist as a producer of food, but not as a frequent neighbour at the food site. This analysis could not be done for two reasons: (i) Except for Ukui, the specialists were too low ranking to score significant joint presences in the control phases. (ii) The effects of benefitting from the specialist on social behaviour happened with a certain delay, thus no clear correlation was found within the specialist phases alone. One might also object that the mere separation of the subgroup from the colony altered its social relationships and that the increased grooming of the specialist was just an accidental reflection of this general change. The objection is implausible because the correlation analysis revealed that 12 such dyads showed an increase and only one a decrease of grooming the specialist. A last objection might be that neighbourhood and grooming are no independent measures of individual associations, since a grooming individual is the nearest neighbour of its partner anyway. Grooming durations however were quite low. In the dyad of the most frequent groomers, Ukui and Junus, grooming was observed in 8% of the time available in the social phases. In all other specialist - non-specialist trials, total grooming time was below 4%. Thus, neighbourhood scores that were recorded during the whole observation time of the social phase of the trials may be analysed as almost independent measures although the two measures surely will correlate to some degree.

Tab. IX indicates that in seven dyadic relationships between a specialist and a non-specialist, namely Ukui-Junus, Topi-Sanah, Rini-Saja, Tjat-Saja, Djalan-Sakri, Djalan-Mayun and Toko-Mayun, both kinds of statistical analyses show significant increases in both affiliation measures. In the dyad Rini-Saja not only the grooming frequencies directed towards the specialist Saja increased, but her grooming of Rini as well. In six of these seven specialist - non-specialist dyads, which reacted both most strongly to the change from specialist to control phases (Wilcoxon rank sum tests) and to differences in their daily scores of joint presence (Kendall τ correlations), the non-specialists ranked among the two non-specialists who profited the most of all other sub-

group members (cf. Tab. V). Topi, who increased grooming and proximity to Sanah, is the only exception. Some of the non-specialists that benefitted most from specialists in the respective subgroups did not increase their affiliative behaviour towards the specialist. Possibly, this would have happened if the experiments had been carried out over a longer period of time. However, the aim of this study is to reveal evidence that monkeys are able to monitor skills of others and not to show that gaining benefit from a partner results in an increase in affiliative behaviour.

Tab X outlines the relative moderate extent of the changes of neighbourhood scores and grooming. Fig. 7 and Fig. 8 show the detailed course of rates and scores. For the dyad Ukui-Junus (Figs. 7.a and 8.a) no data are available for trials 15 to 20 and 90 to 128. For statistical analyses these trials were treated as missing data points. As mentioned above, Djalán probably increased the number of alliances provided to Mayun. It is especially Djalán whose behaviour is the most interesting. First he began to increase his friendly interactions with Sakri, the first of the specialists established in his subgroup. When Mayun became specialist, he switched and began to "flatter" Mayun. Figs. 7 and 8 show how Djalán's grooming and neighbouring depended on the specialist status of both Sakri and Mayun. The Figures provide an additional insight. Djalán continued his special treatment of Sakri even after she had been dismissed as specialist. Obviously he needed several of trials before he realized that the animal with the specialist's role had changed. In summary we may conclude that in six dyads the changes in behavioural treatment of the specialists are reasonably explained by the differential amount of benefit that was gained: A macaque who profits from the feeding skills of another one indeed may increase his affiliation behaviour.

3.11. Duration of Knowledge

The previous sections have shown that group members acquire knowledge of skills of others. How long does it last? Subgroup 1 was available for an

additional trial 6 months after the last regular trial. In the meantime experiments of another project were carried out with this subgroup. Junus, the last of the three specialists of his subgroup, immediately approached the apparatus and manipulated the three levers as if the last trial had taken place only a few days ago, and the other animals refrained from lever manipulations. No chase and only one displacement of Junus by Ketut was observed. Although all subgroup members had the possibility to pull levers with success, Junus performed 93.5% of the total and 100% of the successful lever manipulations. Only Ketut, who as mentioned earlier was taken away from the last 20 trials of subgroup 1 (p 8), was responsible for 6.5% of the unsuccessful manipulations. Obviously low ranking Junus was still remembered as food producer by the other subgroup members. Knowledge of individual competence of other group members is obviously not subject to quick extinction.

4. Discussion

The main questions of this study were: (i) Is it possible to establish low ranking group members as specialized food producers (prediction 1)? (ii) Are other, mainly higher ranking group members able to adapt their behaviour in order to gain benefits (predictions 2 and 3)? (iii) Do changes also occur even in social contexts outside the feeding phase of the trials (predictions 4 and 5)?

(i) All animals trained as specialists succeeded in operating the apparatus regularly and non-specialists ceased to pull levers on their own. The latter simply might be explained by extinction: lever manipulations of non-specialists dropped because they were not rewarded for their incorrect manipulations. However, as soon as they were rewarded again at a one-lever apparatus in the preparatory trial, when the specialist of a former replicate was dismissed (p 12), they started successful manipulations almost immediately.

(ii) The next analysis showed that non-specialists that benefitted from one of the specialists could learn to refrain from displacing and chasing him during the course of a replicate. This finding suggests that non-specialists learned that the specialist's presence at the feeding site was necessary for subsequent food release. It is possible to explain their performance in terms of association learning: the monkeys' knowledge might be of the form "Apparatus plus specialist means release of popcorn". Furthermore, the study provides evidence that non-specialists are able to anticipate the specialist's later actions or effects, as suggested by the increase of following and passing that can be shown for some of the dyads.

(iii) The most interesting finding is that besides these short-term adaptations, the specialists were treated differently in purely social contexts outside

the experimental situation by some of their partners, as a consequence of their activity at the apparatus. In none of the 55 specialist - non-specialist dyads were all affiliative scores reduced, but in seven of them a significant increase in both affiliative measures occurred. In six of the seven dyads the non-specialist was among the two group members who gained the most from the specialist. This makes it very improbable that other reasons than gaining benefit from the specialist induced the increase of sociopositive interaction. One could interpret the increase of neighbourhoods as an extended anticipation of the specialist's role from the feeding to the social phases of the trials, as if his partners assumed that the specialist had other skills in other contexts as well and thus maintained proximity favourable for these other benefits. Increased grooming however cannot be interpreted as simple anticipation of such benefits and suggests that non-specialists associated the positive experience of getting food rewards with the specialized individual who therefore was treated differently even outside the feeding phases. To my knowledge, this is the first study to present evidence for this.

In conclusion: Monkeys are able to assess exceptional and useful capabilities of others. Surprisingly, this assessment seems to be somewhat restricted to a certain location and to other characteristics of the situation. But a few learning opportunities suffice to bring non-specialists to generalize. In one subgroup the knowledge also was remembered for 6 months. The hypothesis and predictions that were formulated in the introductory section were not rejected or contradicted, except that no changes in dominance order occurred.

Kummer (1978) proposed that a member of a primate group should choose his partners according to their optimal qualities and skills. This study shows by experiment that monkeys are indeed able to monitor skills, or at least their effects, of other group members. In earlier studies (Stammach 1978, Stammach & Kummer 1982) we searched for determinant factors that direct group structuring in hamadryas baboons. It appeared, first, that high ranking animals were preferred social partners, in accordance with the model

of Seyfarth (1977). Choice experiments, where the animals could approach their preferred partner without actively being influenced by them or potential competitors, revealed, however, that partners were also selected according to qualities other than rank. The reasons for this attractiveness remained unknown. In this study foraging skill appears as one possible, dominance-independent aspect of attractiveness that changed social interactions. Models of social structure and especially of grooming (see e.g. Seyfarth 1977; Seyfarth 1980; Seyfarth, Cheney & Hinde 1978) should therefore no longer be restricted to dominance rank and aspects of kin relationships (Kurland 1977, Silk et al. 1981). We have to expect that monkeys choose their social partners carefully according to further characteristics.

In discussing the ability of primates to apply their knowledge in order to adjust their responses to others, the role concept is relevant. In descriptions and analyses of functional aspects of behaviour in human and non-human primate groups this concept often appears (see Nagel 1980). It was first introduced to psychology and sociology and applied in primatology later on (e.g. Bernstein & Sharpe 1965, Benedict 1969). According to Benedict a human role "abstracts normative or stereotyped aspects of behaviour from the full repertoire of an individual's actions". Roles in human are defined by expectations of other individuals. Thus there are two criteria defining human role behaviour: (i) a behaviour set that is characteristic for a particular individual and (ii) the expectation or even the insistence of other individuals that a role incumbent will perform these special behaviour patterns. When the role concept is used in animals, the aspect of expectation is difficult to assess and thus is often neglected or replaced. Yet, the concept becomes meaningless if it is used to describe mere idiosyncrasies (Hinde 1978, Nagel 1980). And lastly, role behaviour in animals requires that the behaviour patterns may be observed in incumbents of certain social positions (see Fedigan 1978), that the role activities benefit other group members or the whole group and that it is subject to regulation by the group (Nagel loc. cit.). A given role behaviour is not restricted to certain individuals but former role incumbents may be

replaced by others as e.g. seen in changes of α -positions of males in monkey groups.

The results of this study lead me to conclude that the role concept encompassing expectation is applicable to our macaques. The role of a foodproducer was performed by different incumbents, and it benefited other group members. While these two criteria were experimental artifacts they might well occur in nature to a lesser extent. The essential criterion is the expectation of other group members on the specialist's performance, and it was an original response of the group. However, I observed no indication of insistence on the part of one of the non-specialists, e.g. seeking out an absent specialist or dragging him toward the apparatus. If one accepts this version of the role concept for the present study, we have found, in monkeys, a necessary component of a society with optimized division of labour among differently skilled individuals.

The study suggests that partners that seek benefit from others tend to improve their relationships with them, as indicated by the increase of grooming given to the specialist and the maintenance of spatial proximity even at times when no benefit was obtained. The correlation between intimacy of a social relationship and its task performance has been the focus of older studies. Animals were forced into a division of labour or cooperation (e.g. Boren 1966, Wechkin 1970, Mason & Hollis 1961). Two main results emerged. (i) Animals often ceased to cooperate in laboratory experiments in which alternately one of the two individuals had to perform a simple learning task whereupon his partner got a reward. They improved their performance only if they were rewarded with low latency for their own activities. This point will be discussed later (p 39). (ii) Familiar monkeys were more successful in cooperating than unfamiliar ones. The methodical approach of these studies was the reverse of the present one: Intimacy led to better cooperation whereas in this study animals increased their intimacy to the specialist because they coacted with him and perhaps in order to benefit from his activities.

Further studies tested the hypothesis that animals occupying a useful position in the group may increase their dominance rank. Beck (1972 and 1973) in his study on cooperative tool use in captive baboons found no evidence of increased dominance rank of the tool using animal. In a study of Miller, Murphy and Mirsky (1955), however, a low ranking rhesus monkey of a group of ten rose in rank when he was used as a stimulus animal announcing painful events to its group peers. Each time before one of his group peers received an electric shock when he was sitting in a test chamber, the adjacent cage where the stimulus monkey was sitting was illuminated. These findings suggest that monkeys may raise in rank if they become an important aversive stimulus for their group companions. However, we may doubt whether an animal will improve its rank in an experimental situation where it becomes a positive non-punitive conditioned stimulus as in this study. This would have to be tested by establishing specialists that would produce the most of a group's food.

Comparing the "specialist" and the "non-specialist" strategies that emerge due to the experimental setting, we may ask which of both strategies would be favoured by the evolutionary process if we take this experiment as a model of a foraging task in which the specialist is an individual extremely skilled in searching and gathering food while other group members benefit from his skills. For the following argument I assume that the specialist does not obtain more food than the average non-specialist, for example because he arrives first at the food site. Both the specialist and the non-specialists have a gain in energy that may be turned into offspring, but the net gain of the specialist per quantity of food eaten is smaller since he expends more time and energy in food gathering than he would invest to satisfy his own needs. He gains less direct fitness than the other group members but increases their fitness by his activity. The specialist, however, could refrain from producing or searching food and play the "non-specialist" strategy too; but in this case, he would lose all his benefit for saving only little supplementary costs. There is no possibility for the specialist to get rid of a benefitting partner, since he cannot threaten away the higher ranking group peer. Thus, he is expected to continue

his unselfish behaviour. Under the assumption that the "specialist" strategy pays less than the "non-specialist" one we should expect that the "specialist" strategy disappears from a hypothetical population. There is, however, a possibility to equalize the pay offs of the two strategies: the concept of reciprocal altruism (Trivers 1971, Packer 1977) or mutualism (Brown 1983) predicts that non-relatives should perform cooperative or even altruistic acts if they will receive compensatory acts in their turn and if there is a discrimination against cheating individuals who accept help but refuse to repay it. The results of the cooperation experiments (Boren, Wechkin, Mason & Hollis, loc. cit.) seem to confirm this suggestion on a proximate level, since successful cooperation occurred only if compensatory acts were rendered with a short delay. In the present experiments we may expect a repayment by the non-specialists even though the specialist was not altruistic in the given artificial situation. Kurland (1977), Dawkins (1976) and Silk (1982) have claimed that social grooming is a short-term altruistic act since it conveys benefit to the recipient and costs to the performer. In this study, an increase of grooming the specialist contingent with the nutrient benefit was observed in some of his partners. Grooming thus might be the repayment of received benefits. The benefits of grooming are easily seen since grooming removes ectoparasites. Furthermore, being groomed with a dominant non-specialist and thus sitting near him probably reduces the rate of being attacked by others during the grooming session. It is harder to find convincing costs to the donor. A first hint that grooming not only serves fur cleaning is suggested by the fact that time spent grooming usually exceeds time that would be necessary to remove parasites. Dunbar & Sharman (1984) hypothesize that the most plausible costs would be a loss of time that otherwise could be spent for acquiring resources that can be transformed into offspring. They found in two species of old world monkeys that social time that was needed for grooming was maintained at the expense of resting time, if feeding time had to be increased. This suggests that either the costs of grooming are trivial or that grooming is valuable to the groomer in terms of long-term benefits in the formation and maintenance of good relationships and alliances. I agree with Dunbar & Sharman that grooming is no

candidate for an altruistic repayment of debts, since altruistic costs of grooming are negligible. I rather hypothesize that grooming in primates serves to maintain and establish social bonds. These serve as a lasting intervening variable for a later repayment of given altruistic acts even with a considerable delay (see Kaplan 1978, Seyfarth & Cheney 1984). Axelrod & Hamilton (1981) were able to demonstrate by a computer simulation based on the "prisoner's dilemma game" that cooperation based on reciprocity may evolve under the condition that two individuals will meet potential altruistic situations repeatedly. If we assume that grooming is an instrument for improving social relations to others and regardless whether it is short-term altruism by itself we can argue that the amount of grooming that is observed from A to B is an indicator of B's value to A and thus an indicator of the strength of the social bond as desired by A. The frequent proximity and mutual availability of bonded partners guarantees a high probability of mutual exchange of help. A close social relationship thus can be treated as a convention among two animals to exchange mutual help and assistance. Referring to the present study I thus hypothesize that the increase of grooming provided to the specialist is not the repayment of the act of food sharing itself but rather to assure the specialist's tolerance.

5. Summary

The aim of this study was to investigate the capability of monkeys to assess special characteristics in conspecifics. In a first phase I ascertained that all members of a colony of longtailed macaques (*Macaca fascicularis*) were able to attain food by manipulating a one lever apparatus, thus introducing the "tradition" of lever pulling. Then, experiments were carried out on subgroups of the colony where only one of the lower ranking subgroup members was trained to succeed in a more complex task where three levers had to be pulled in a correct sequence. Eight specialists were established in sequence. These specialists became food producers for themselves and for the other group members. Each trial of a specialist's series was carried out in two phases. In the first, the food phase, the food dispensing apparatus was active and responses of other subgroup members to the food producing specialist were observed. In the second, the social phase, the apparatus remained inactive and observations focused on social interactions of the subgroup. As expected, primarily high ranking subgroup members attempted to participate in the food rewards gained by the specialist. It is shown that high ranking animals began to hold back their initial chasing of the specialist from the food site in course of the trials and were soon tolerated to sit near the subordinate food producer. Furthermore, some of the non-specialists began to follow or even to pass the specialist when he was approaching the apparatus to manipulate the levers. These non-specialists thus indicated that they were able to anticipate later actions. In seven out of 55 specialist - non-specialist relationships all predicted changes in social interactions occurred. In the majority of the dyads in which a change in social affiliation was registered an increase of grooming or spatial proximity was positively correlated with the amount of benefit gained from the specialist. In the social phase of the trials the non-specialists gave more grooming to the food producers and maintained spatial proximity even in this

second phase. To conclude: At least some of the group members became aware of the skills of the specialists and adapted their behaviour accordingly as if to maximize benefits from their skills.

Previous studies had already suggested that monkeys know about social position, social relationships and kinship of group members. This study adds a new aspect of knowledge, namely knowledge on capabilities and skills of others. Differential knowledge allows monkeys to select partners optimally according to their skills and social position.

6. References

- Altmann, J. (1974): Observational study of behavior: sampling methods. *Behaviour* 49: 227-267.
- Altmann, S. (1974): Baboons, space, time, and energy. *Amer. Zool.* 14: 221-248.
- Angst, W. (1974): Das Ausdrucksverhalten der Javaneraffen. *Advances in Ethology* Vol. 15. Paul Parey, Berlin Hamburg.
- Axelrod, R. & W.D. Hamilton (1981): The evolution of cooperation. *Science* 211: 1390-1396.
- Bachmann, Ch. & H. Kummer (1980): Male assessment of female choice in hamadryas baboons. *Behav. Ecol. Sociobiol.* 6: 315-321.
- Beck, B. (1972): Tool use in captive hamadryas baboons. *Primates* 13: 276-296.
- Beck, B. (1973): Cooperative tool use by captive hamadryas baboons. *Science* 182: 594-597.
- Beckmann, E. & R. Jeschke (1980): Einführung in die Digitalelektronik 1. Verlagsgesellschaft Schulfernsehen, Köln.
- Beckmann, E. & R. Jeschke (1981): Einführung in die Digitalelektronik 2. Verlagsgesellschaft Schulfernsehen, Köln.
- Benedict B. (1969): Role analysis in animals and men. *Man* 4: 203-214.
- Bernstein, I.S. & L.G. Sharpe (1965): Social roles in a rhesus monkey group. *Behaviour* 26: 1-2.
- Boren, J.J. (1966): An experimental social relation between two monkeys. *J. Exp. Anal. Behav.* 9: 691-700.
- Brown, J.L. (1983): Cooperation - a biologist's dilemma. *Adv. Stud. Behav.* 13: 1-37.
- Cheney, D.L. & R.M. Seyfarth (1980): Vocal recognition in free-ranging vervet monkeys. *Anim. Behav.* 28: 362-367.
- Clutton-Brock, T.H. & T.H. Harvey (1977): Primate ecology and social organization. *J. Zool. London* 183: 1-39.
- Crook, J.H. (1970): Social organization and the environment: aspects of contemporary social ethology. *Anim. Behav.* 18: 197-209.
- Dasser, V. (in press): A social concept in Java monkeys. *Anim. Behav.*

- Dawkins, R. (1976): The selfish gene. Oxford University Press, Oxford.
- Dunbar, R.I.M. & M. Sharman (1984): Is social grooming altruistic? *Z. Tierpsychol.* 64: 163-173.
- Fedigan, L.M. (1976): A study of roles in the Arashiyama west troop of Japanese monkeys (*Macaca fuscata*). *Contributions to Primatology* Vol. 9. Karger, Basel.
- Hachet, T. (1974): Un distributeur automatique de nourriture pour l'étude du comportement alimentaire du porc. *Physiology & Behavior* 12: 515-517.
- Hinde, R. (1974): Interactions, relationships and social structure in non-human primates. *Symp. 5th Cong. Int'l. Primat. Soc., Nagoya Japan*, pp 13-24.
- Hinde, R.A. (1978): Dominance and role - two concepts with dual meanings. *J. Social Biol. Struct.* 1: 27-38.
- IMSL-Library (1979): Reference Manual. International Mathematical & Statistical Libraries Inc., Houston, Texas, USA.
- Jorde L.B. & J.N. Spuhler (1974): A statistical analysis of selected aspects of primate demography, ecology, and social behavior. *J. Anthropol. Res.* 30: 199-224.
- Kaplan, J.R. (1978): Fight interference and altruism in rhesus monkeys. *Amer. J. Phys. Anthropol.* 49: 241-249.
- Kummer, H. (1971): Primate societies. Group techniques of ecological adaptation. Chicago Ill. / NY, Aldine Atherton.
- Kummer, H. (1978): On the value of social relationships to nonhuman primates: A heuristic scheme. *Social Science Information* 17: 687-705.
- Kurland, J.A. (1977): Kin selection in the Japanese monkey. *Contributions to Primatology* Vol. 12, Karger, Basel, pp 145.
- Lienert G.A. (1973): Verteilungsfreie Methoden der Biostatistik, Band I. Anton Hain, Meisenheim am Glan. pp 736.
- Mason, W.A. & J.H. Hollis (1961): Communication between young rhesus monkeys. *Anim. Behav.* 9: 211-221.
- Meier, G.W., H.C. Wilcoxon, R. Orlando & D.C. Paulson (1968): The development of food-reinforced behaviors in a social situation. *Proc. 2nd int. Congr. Primat., Atlanta, GA. Vol. I*, pp 143-148. Karger, Basel.
- Miller, R.G., Jr. (1964): A trustworthy jackknife. *Ann. Math. Stat.* 35: 1594-1605.

- Miller, R.E., J.V. Murphy & I.A. Mirsky (1955): The modification of social dominance in a group of monkeys by interanimal conditioning. *J. Comp. Physiol. Psychol.* 48: 392-396.
- Mosteller, F. & J.W. Tukey (1977): *Data analysis and regression*. Addison Wesley Publishing Company, Reading Massachusetts.
- Nagel, U. (1979): On describing primate groups as systems: the concept of ecosocial behavior. In: I.S. Bernstein & E.O. Smith (eds.): *Primate Ecology and Human Origins: Ecological Influences on Social Organization*. Garland Press, New York & London. pp 313-339.
- Nagel, U. (1980): *Beiträge zur Biologie der funktionellen Verhaltensdifferenzierung in Primatengruppen*. Dissertation Universität Zürich.
- Packer, C. (1977): Reciprocal altruism in *Papio anubis*. *Nature* 265: 441-443.
- SAS User's Guide (1982a): *Basics*. SAS Institute Inc., Cary, North Carolina, pp 921.
- SAS User's Guide (1982b): *Statistics*. SAS Institute Inc., Cary, North Carolina, pp 584.
- SASGRAPH User's Guide (1981). SAS Institute Inc., Cary, North Carolina, pp 126.
- Seyfarth, R.M. (1977): A model of social grooming among adult female monkeys. *J. Theor. Biol.* 65: 671-698.
- Seyfarth, R.M. (1980): The distribution of grooming and related behaviours among adult female vervet monkeys. *Anim. Behav.* 28: 798-813.
- Seyfarth, R.M., D.L. Cheney & R. Hinde (1978): Some principles relating social interactions and social structure among primates. In: D.J. Chivers & J. Herbert (eds.): *Recent Advances in Primatology*, Academic press, London. pp. 39-51.
- Seyfarth, R.M. & D.L. Cheney (1984): Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* 308: 541-543.
- SIEMENS (1983): *Operating System BS3000, FORTRAN 77, user's guide*. Siemens AG, Manual Editing Group, München.
- Silk, J.B. (1982): Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour* 79: 162-188.

- Silk, J.B., A. Samuels & P.S. Rodman (1981): The influence of kinship, rank and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behaviour* 78: 111-137.
- Stammbach, E. (1978): On social differentiation in groups of captive female hamadryas baboons. *Behaviour* 67: 322-338.
- Stammbach, E. & H. Kummer (1982): Individual contributions to a dyadic interaction: an analysis of baboon grooming. *Anim. Behav.* 30: 964-971.
- Trivers, R.L. (1971): The evolution of reciprocal altruism. *Quart. Rev. Biol.* 46: 35-55.
- Waal, F. de (1977): The organization of agonistic relations within two captive groups of Java monkeys (*Macaca fascicularis*). *Z. Tierpsychol.* 44: 225-282.
- Wechkin, St. (1970): Social relationships and social facilitation of object manipulation in *Macaca mulatta*. *J. Comp. Physiol. Psychol.* 73: 456-460.

7. Zusammenfassung

Diese Studie über kognitive Fähigkeiten von Primaten untersucht, ob Javaneraffen (*Macaca fascicularis*) Eigenschaften und insbesondere spezielle Fähigkeiten von anderen Artgenossen einschätzen können und ihr Verhalten so anzupassen wissen, dass sie von deren Fähigkeiten profitieren. Bevor die eigentlichen Experimente durchgeführt wurden, trainierte ich alle Tiere einer Javaneraffen-Kolonie darauf hin, sich an einer einfachen Apparatur durch Bedienung eines Hebels Futter zu beschaffen. Damit war allen Kolonienmitgliedern das Prinzip "Hebelziehen" bekannt. Die Experimente wurden daraufhin an Untergruppen der Kolonie durchgeführt. In acht Versuchsserien wurde jeweils ein tiefrangiges Untergruppenmitglied an einer komplexeren Apparatur trainiert, drei Hebel in einer korrekten Sequenz zu ziehen, worauf die Apparatur eine grössere Futterbelohnung ausschüttete, von der nicht nur dieses Individuum, sondern auch andere Gruppenmitglieder fressen konnten. Das speziell trainierte Individuum wurde damit zum Futterlieferanten für sich und seine Gruppenmitglieder. Jeder Einzelversuch wurde in zwei Phasen durchgeführt. In einer ersten, der Futterphase, war der Futter liefernde Apparat eingeschaltet und die Reaktionen der anderen Gruppenmitglieder auf den Futter produzierenden Spezialisten wurden beobachtet. In der zweiten, der Sozialphase, war der Apparat ausgeschaltet und die Beobachtungen richteten sich auf das soziale Verhalten der anderen Gruppenmitglieder gegenüber dem Spezialisten.

Wie zu erwarten war, versuchten vor allem hochrangige Untergruppenmitglieder an dem vom Spezialisten produzierten Futter teilzuhaben. Diese hochrangigen Tiere jagten vorerst den Spezialisten von der Apparatur weg, um zum Futter zu kommen, lernten aber im Verlauf der Versuche ihr Jagen zu reduzieren und gar ganz aufzuhören. Einige der Nichtspezialisten begannen überdies, dem Spezialisten zu folgen oder ihn gar zu überholen, sobald dieser sich der Apparatur näherte. Dies ist ein Hinweis, dass diese Nichtspezialisten künftige Handlungen des Spezialisten voraussehen können.

In sieben von 55 Spezialist-Nichtspezialist-Dyaden konnten zudem in der Sozialphase der Versuche Änderungen in den sozialen Interaktionen festgestellt werden, von denen sechs mit grosser Sicherheit auf die spezielle Position des Futterproduzenten zurückzuführen sind. Sechs Nichtspezialisten, die in ihrer jeweiligen Untergruppe am meisten vom Spezialisten profitierten, liessen diesem vermehrt soziale Hautpflege zukommen und hielten sich zudem auch während der Sozialphase häufiger in seiner Nähe auf, wie mit der Methode der nächsten Nachbarschaften gezeigt werden konnte. Daraus ist zu schliessen, dass mindestens ein Teil der Untergruppenmitglieder das Können des Spezialisten erkannte, passten sie doch ihr Verhalten in einer Art und Weise an, dass sie ihren Nutzen maximieren konnten.

Andere Studien hatten bereits darauf hingewiesen, dass Affen über Wissen über soziale Position, soziale Beziehungen und Verwandtschaftsverhältnisse verfügen. Die vorliegende Studie fügt einen neuen Aspekt des Wissens hinzu, nämlich das Wissen über Fähigkeiten und Können anderer. Das differenzierte Wissen über potentielle Partner erlaubt es einem Affen, seine Partner bezüglich Fähigkeiten und sozialer Position optimal auszuwählen.

8. *Ethogram*

Behavioural item	Definition *)
alliance	A threatens or chases a third animal that already was threatened or chased by R at most 2 sec. ago.
approaching apparatus	A walks or runs within area 2 least 1 m in direction of the apparatus and finally enters area 1 of the enclosure
bared teeth grin	A retracts upper and lower lips, baring his teeth
chasing	A runs after R, for at least 1 m while R is fleeing. A often threatens R
chasing from apparatus	A threatens or chases R who is staying in area 1 (food site). R leaves within 2 sec. at most.
displacing from apparatus	A enters area 1 of the enclosure where R is sitting. R leaves area 1 at most 2 sec. later.
following	A moves in the same direction behind R for at least 1 m without deviating from R's route more than 20°

grooming	A manipulates R's hair with 1 or 2 hands
head bob threat	A thrusts the head forward towards R without locomotion
nearest neighbour	R is the nearest neighbour of A. The maximal distance between A and R is 7.2 m.
open mouth threat	A stares R with open mouth.
passing	A first follows R and then passes, whereupon R follows A.
supplanting	A approaches R closer than 50 cm. Within at most 2 sec after A has crossed the 50 cm line, R leaves A.

*) A = Actor, R = Recipient

Tables

and

Figures

Table I.

Characteristics of subjects, subgroup composition

Subgroup	Name	Abbreviation	Approx. age	Birth date	Sex	Offspring of	Dominance *) rank in subgroup
1	Ketut	KT	6	8. 9. 1977	Male	Sakri	1
	Titin	TT	13	1970	Female	Sangi	2
	Salim	SL	4	5. 7. 1979	Male	Sakri	3
	Ukui	UK	2	10. 7. 1981	Male	Upit	4
	Malen	ML	3 1/2	13. 3. 1980	Male	Dana	5
	Junus	JN	3	29. 9. 1980	Male	Titin	6
	Subali	SB	3	26. 10. 1980	Male	Sakri	7
2	Rini	RN	5	12. 8. 1980	Female	Timor	1
	Tjat	TJ	3 1/2	21. 3. 1982	Female	Timor	2
	Topi	TP	9	7. 7. 1976	Female	Timor	3
	Sanah	SN	6	8. 5. 1979	Female	Dili	4
	Saja	SJ	2 1/2	27. 2. 1983	Female	Sanah	5
	Jumi	JM	5	27. 7. 1980	Female	Upit	6
	Djambi	DJ	4 1/2	5. 1981	Female	Dana	7
	Sapi	SP	3 1/2	8. 3. 1982	Female	Sakri	8
3	Topi	TP	8	7. 7. 1976	Female	Timor	1
	Toko	TK	2 1/2	2. 5. 1982	Male	Topi	2
	Dili	DL	9 1/2	26. 5. 1975	Female	Timor	3
	Djalan	DA	2 1/2	11. 4. 1982	Male	Dili	4
	Mayun	MY	8 1/2	25. 4. 1976	Female	Ambon	5
	Upit	UP	9 1/2	28. 5. 1975	Female	Ambon	6
	Titin	TT	14	1970	Female	Sangi	7
	Sakri	SK	11	15. 8. 1973	Female	Dana	8
	Sapi	SP	2 1/2	8. 3. 1982	Female	Sakri	9

*) cf. Tab. III.

Table II.

Replicates and specialists

Subgroup	Specialist	Number of trials	Total experimental time (hours)	Trial Numbers	Observation period
1	Malen	47	35.0	14 - 60	June 83 - Sept 83
	Ukui	39	35.0	74 - 113	Oct 83 - Jan 84
	Junus	70	52.0	134 - 203	Feb 84 - June 84
2	Sanah	41	31.0	516 - 556	June 85 - Sept 85
	Djambi	34	27.75	567 - 600	Oct 85 - Nov 85
	Saja	55	41.0	607 - 661	Dec 85 - Mar 86
3	Sakri	30	29.66	320 - 353	Sept 84 - Oct 84
	Mayun	97	83.0	357 - 453	Nov 84 - May 85

Table III.

Dominance ranks in subgroups: Numbers of bared teeth grins per dyad. The animals are arranged according to decreasing dominance rank.

Subgroup 1:

Actor	Recipient						
	Ketut	Titin	Salim	Ukui	Malen	Junus	Subali
Ketut	-	4	3		2	2	
Titin	6	-		1			
Salim	4	28	-	1			
Ukui	39	3	51	-			
Malen	31	25	36	3	-	1	1
Junus	20		19	14	2	-	
Subali	19	10	19	1	15	21	-

Subgroup 2:

Actor	Recipient							
	Rini	Tjat	Topi	Sanah	Saja	Jumi	Djambi	Sapi
Rini	-							
Tjat	27	-						
Topi	62	37	-					
Sanah	8	6	8	-				
Saja	17	8	23	1	-			
Jumi	18	7	5	14	4	-		
Djambi	23	9	10	41	3	8	-	
Sapi	5	7	5	19	3	6	27	-

Subgroup 3:

Actor	Recipient								
	Topi	Toko	Dili	Djalan	Mayun	Upit	Titin	Sakri	Sapi
Topi	-								
Toko	1	-							
Dili		5	-						
Djalan	9	12		-					
Mayun	57	20	99	22	-	2			
Upit	2	2	6	2	12	-			
Titin	5		13	3	5	5	-		
Sakri	9	3	73	11	39	3	4	-	
Sapi			18	3	24	15	2	1	-

Table IV.

Kendall τ coefficients describing the correlations between neighbourhood scores as observed in the whole group and neighbourhood scores and grooming rates as observed in the subgroups. t-values are given according to Miller's jackknife (see text).

Subgroup	Variables		
	neighbourship subgroup - grooming subgroup	neighbourship subgroup - neighbourship colony	grooming subgroup - grooming colony
1	$\tau = 0.39$ $t=2.36$ *	$\tau = 0.33$ $t=1.61$ ns	$\tau = 0.08$ $t=0.24$ ns
2	$\tau = 0.50$ $t=8.17$ **	$\tau = 0.09$ $t=0.41$ ns	$\tau = -0.05$ $t=0.71$ ns
3	$\tau = 0.56$ $t=6.20$ **	$\tau = 0.52$ $t=3.37$ **	$\tau = 0.41$ $t=6.53$ **

ns: not significant

*: significant at 5% level

**: significant at 1% level

Table V.

Number of trials per replicate when the two dyad members were present together at the apparatus at least once in a trial and number of intervals per replicate when both were present. Dyads are arranged according to their sum of joint presence.

Group member	Specialist		Total number of trials per replicate	Number of trials together	% of trials together	% of intervals together
Ketut	Malen	+	47	43	91.5	30.05
Salim	Malen	+	47	43	91.5	24.57
Ukui	Malen	+	47	36	76.6	8.81
Junus	Malen		47	39	82.9	6.73
Titin	Malen	+	47	29	61.7	4.10
Subali	Malen		47	10	21.3	1.10
Ketut	Ukui	+	39	27	69.2	11.78
Junus	Ukui		39	30	77.0	9.66
Malen	Ukui		39	28	71.8	9.24
Salim	Ukui	+	39	22	56.4	4.85
Titin	Ukui	+	39	15	38.5	4.85
Subali	Ukui		39	4	10.3	0.10
Ukui	Junus	+	70	68	97.1	17.37
Malen	Junus	+	70	50	71.4	11.71
Salim	Junus	+	70	57	81.4	10.46
Ketut	Junus	+	70	17	24.3	0.76
Titin	Junus	+	70	17	24.8	0.75
Subali	Junus		70	6	8.6	0.17
Saja	Sanah		41	34	82.9	5.38
Rini	Sanah	+	41	20	48.8	1.93
Tjat	Sanah	+	41	20	48.8	1.21
Topi	Sanah	+	41	5	12.2	0.60
Sapi	Sanah		41	2	4.8	0.04
Djambi	Sanah		41	1	2.4	0.02
Jumi	Sanah		41	1	2.4	0.02
Saja	Djambi	+	34	24	68.6	5.09
Tjat	Djambi	+	34	10	28.6	0.39
Sanah	Djambi	+	34	5	14.3	0.37
Sapi	Djambi		34	4	11.4	0.37
Jumi	Djambi	+	34	5	14.3	0.35
Rini	Djambi	+	34	5	14.3	0.28
Topi	Djambi	+	34	0	0	0
Tjat	Saja	+	55	50	91.0	7.95
Rini	Saja	+	55	49	89.1	7.13
Topi	Saja	+	55	29	52.7	2.15
Sanah	Saja	+	55	16	29.1	0.88
Sapi	Saja		55	5	9.0	0.33
Jumi	Saja		55	3	5.5	0.15
Djambi	Saja		55	1	1.8	0.01
Djalan	Sakri	+	30	25	83.3	6.65
Sapi	Sakri		30	15	50	1.04
Toko	Sakri	+	30	15	50	0.95
Topi	Sakri	+	30	5	16.6	0.13
Upit	Sakri	+	30	1	3.3	0.09
Mayun	Sakri	+	30	2	6.7	0.07
Dili	Sakri	+	30	2	6.7	0.06
Titin	Sakri	+	30	0	0	0
Djalan	Mayun	+	97	87	89.7	8.88
Toko	Mayun	+	97	82	84.5	6.57
Topi	Mayun	+	97	59	60.8	3.00
Dili	Mayun	+	97	46	47.4	1.56
Upit	Mayun		97	11	11.3	0.24
Sapi	Mayun		97	8	8.2	0.31
Sakri	Mayun		97	8	8.2	0.30
Titin	Mayun		97	0	0	0

+: group member ranks higher than specialist

Table VI.

Kendall τ correlations between leaving the apparatus after displacements and chasings per total number of leavings and trial numbers for the 8 specialists

Subgroup	Specialist	displacing	chasing
1	Malen	-0.32 **	-0.30 *
	Ukui	-0.09 ns	-0.32 **
	Junus	-0.08 ns	-0.15 ns
2	Sanah	-0.40 **	-0.51 **
	Djambi	-0.08 ns	-0.50 **
	Saja	-0.08 ns	-0.37 **
3	Sakri	-0.05 ns	-0.01 ns
	Mayun	-0.14 ns	-0.29 **

ns: not significant

*: significant at 5% level

**: significant at 1% level

Table VII.

Kendall τ correlations between number of displacements and chasings from the apparatus per presence of the specialist and trial numbers. Dyads are arranged according to their sum of joint presence.

Group member	Specialist		Displacing	Chasing
Ketut	Malen	+	-0.31 **	-0.36 **
Salim	Malen	+	-0.29 **	-0.21 *
Ukui	Malen	+	ns	--
Junus	Malen		ns	ns
Titin	Malen	+	ns	ns
Subali	Malen		--	--
Ketut	Ukui	+	-0.52 **	-0.42 **
Junus	Ukui		--	--
Malen	Ukui		-0.25 *	--
Salim	Ukui	+	ns	-0.33 **
Titin	Ukui	+	ns	--
Subali	Ukui		--	--
Ukui	Junus	+	ns	ns
Malen	Junus	+	--	--
Salim	Junus	+	ns	ns
Ketut	Junus	+	-0.20 *	ns
Titin	Junus	+	ns	-0.23 *
Subali	Junus		--	--
Saja	Sanah		ns	--
Rini	Sanah	+	-0.53 **	-0.38 **
Tjat	Sanah	+	-0.36 **	-0.51 **
Topi	Sanah	+	-0.26 *	-0.33 **
Sapi	Sanah		--	--
Djambi	Sanah		--	--
Jumi	Sanah		--	--
Saja	Djambi	+	ns	ns
Tjat	Djambi	+	ns	-0.48 **
Sanah	Djambi	+	ns	ns
Sapi	Djambi		--	--
Jumi	Djambi	+	ns	--
Rini	Djambi	+	ns	ns
Topi	Djambi	+	--	ns
Tjat	Saja	+	-0.30 **	-0.40 **
Rini	Saja	+	ns	-0.50 **
Topi	Saja	+	-0.27 **	-0.23 **
Sanah	Saja	+	--	--
Sapi	Saja		--	--
Jumi	Saja		--	--
Djambi	Saja		--	--
Djalan	Sakri	+	-0.45 **	--
Sapi	Sakri		--	--
Toko	Sakri	+	ns	ns
Topi	Sakri	+	ns	ns
Upit	Sakri	+	--	ns
Mayun	Sakri	+	ns	ns
Dili	Sakri	+	ns	ns
Titin	Sakri	+	--	--
Djalan	Mayun	+	-0.40 **	-0.22 **
Toko	Mayun	+	-0.32 **	-0.25 **
Topi	Mayun	+	ns	ns
Dili	Mayun	+	-0.22 **	-0.32 **
Upit	Mayun		--	--
Sapi	Mayun		--	--
Sakri	Mayun		--	--
Titin	Mayun		--	--

+: group member ranks higher than specialist
 --: insufficient amount of data
 ns: not significant
 *: significant at 5% level
 **: significant at 1% level

Table VIII.

Kendall τ correlations between number of followings and passings of others per number of approaches of the apparatus by the specialist and trial numbers. Dyads are arranged according to their sums of joint presence.

Group member	Specialist		Following	Passing
=====				
Saja	Sanah		0.37 **	0.33 **
Rini	Sanah	+	ns	ns
Tjat	Sanah	+	ns	--
Topi	Sanah	+	--	--
Sapi	Sanah		ns	--
Djambi	Sanah		--	--
Jumi	Sanah		--	--

Saja	Djambi	+	ns	ns
Tjat	Djambi	+	ns	--
Sanah	Djambi	+	ns	--
Sapi	Djambi		ns	ns
Jumi	Djambi	+	--	--
Rini	Djambi	+	ns	--
Topi	Djambi	+	--	--

Tjat	Saja	+	0.27 **	ns
Rini	Saja	+	0.36 **	--
Topi	Saja	+	ns	--
Sanah	Saja	+	ns	--
Sapi	Saja		--	--
Jumi	Saja		--	--
Djambi	Saja		--	--
=====				
Djalan	Sakri	+	0.59 **	0.33 *
Sapi	Sakri		ns	0.40 **
Toko	Sakri	+	0.39 **	0.33 *
Topi	Sakri	+	--	ns
Upit	Sakri	+	ns	--
Mayun	Sakri	+	ns	--
Dili	Sakri	+	ns	--
Titin	Sakri	+	--	--

Djalan	Mayun	+	ns	ns
Toko	Mayun	+	0.16 *	ns
Topi	Mayun	+	0.20 **	ns
Dili	Mayun	+	ns	ns
Upit	Mayun		ns	--
Sapi	Mayun		ns	--
Sakri	Mayun		ns	--
Titin	Mayun		--	--
=====				

+: group member ranks higher than specialist
 --: insufficient amount of data
 ns: not significant
 *: significant at 5% level
 **: significant at 1% level

Table IX.

Scores of Wilcoxon rank sum tests and Kendall τ correlation coefficients measuring the relation between status of specialists and neighbourhood scores and grooming rates. For Wilcoxon tests the significance probabilities are given. A negative probability indicates a lower neighbourhood score or grooming rate during the specialist phase. Dyads are arranged according to the sum of joint presence.

Data		Neighbourships		Grooming given to specialist		Grooming received from specialist	
Group member	Specialist	Wilcoxon rank test	Kendall τ coeff.	Wilcoxon rank test	Kendall τ coeff.	Wilcoxon rank test	Kendall τ coeff.
Ketut	Malen	+ ns	ns	ns	ns	ns	ns
Salim	Malen	+ -0.02	-0.18 *	ns	ns	ns	ns
Ukui	Malen	+ 0.02	ns	ns	ns	ns	ns
Junus	Malen	ns	ns	ns	ns	ns	ns
Titin	Malen	+ ns	ns	ns	ns	ns	ns
Subali	Malen	ns	ns	ns	ns	ns	ns
Ketut	Ukui	+ ns	ns	ns	ns	ns	ns
Junus	Ukui	ns	ns	ns	ns	ns	ns
Malen	Ukui	0.02	0.17 *	ns	ns	ns	ns
Salim	Ukui	+ ns	ns	ns	ns	ns	ns
Titin	Ukui	+ -0.02	-0.16 *	ns	ns	ns	ns
Subali	Ukui	ns	ns	ns	ns	ns	ns
Ukui	Junus	+ 0.01	0.20 **	0.02	0.23 **	ns	ns
Malen	Junus	+ ns	ns	ns	ns	ns	ns
Salim	Junus	+ ns	ns	ns	ns	ns	ns
Ketut	Junus	+ -0.02	ns	ns	ns	ns	ns
Titin	Junus	+ 0.02	ns	ns	ns	ns	ns
Subali	Junus	ns	ns	ns	ns	ns	ns
Saja	Sanah	ns	ns	-0.04	-0.14 *	-0.02	-0.16 *
Rini	Sanah	+ ns	ns	ns	ns	ns	ns
Tjat	Sanah	+ 0.03	ns	ns	ns	ns	ns
Topi	Sanah	+ 0.01	0.18 *	0.01	0.31 **	ns	0.26 **
Sapi	Sanah	-0.01	ns	-0.01	ns	ns	ns
Djambi	Sanah	-0.02	ns	ns	ns	ns	ns
Jumi	Sanah	ns	ns	0.05	ns	0.02	ns
Saja	Djambi	+ 0.01	0.31 **	ns	ns	ns	ns
Tjat	Djambi	+ 0.04	ns	ns	ns	ns	ns
Sanah	Djambi	+ -0.01	ns	ns	ns	ns	ns
Sapi	Djambi	ns	ns	ns	ns	ns	ns
Jumi	Djambi	+ -0.01	ns	ns	ns	ns	ns
Rini	Djambi	+ ns	ns	ns	ns	ns	ns
Topi	Djambi	+ ns	ns	ns	ns	ns	ns
Tjat	Saja	+ 0.01	0.25 **	0.04	0.17 *	ns	ns
Rini	Saja	+ 0.01	0.27 **	0.01	0.27 **	0.01	0.19 **
Topi	Saja	+ 0.01	0.19 **	ns	0.17 *	ns	ns
Sanah	Saja	+ ns	ns	0.01	0.19 **	ns	ns
Sapi	Saja	ns	ns	ns	0.21 **	ns	ns
Jumi	Saja	ns	ns	ns	ns	-0.03	ns
Djambi	Saja	ns	ns	ns	ns	ns	ns
Djalan	Sakri	+ 0.01	0.20 *	0.01	0.28 **	ns	ns
Sapi	Sakri	ns	ns	ns	ns	ns	0.15 *
Toko	Sakri	+ ns	ns	ns	ns	ns	ns
Topi	Sakri	+ ns	ns	0.01	ns	0.01	ns
Upit	Sakri	+ ns	ns	ns	0.21 *	ns	ns
Mayun	Sakri	+ ns	ns	ns	ns	ns	ns
Dili	Sakri	+ ns	ns	0.01	ns	0.01	ns
Titin	Sakri	+ ns	ns	ns	ns	ns	ns
Djalan	Mayun	+ 0.01	0.34 **	0.01	0.28 **	ns	ns
Toko	Mayun	+ 0.01	0.29 **	0.02	0.25 **	ns	ns
Topi	Mayun	+ ns	-0.15 *	0.04	ns	-0.01	-0.15 *
Dili	Mayun	+ ns	0.19 **	0.01	0.25 **	-0.01	ns
Upit	Mayun	ns	ns	ns	ns	ns	ns
Sapi	Mayun	ns	ns	ns	ns	ns	ns
Sakri	Mayun	ns	ns	ns	ns	ns	ns
Titin	Mayun	-0.01	ns	ns	ns	-0.01	ns

+: group member ranks higher than specialist

ns: not significant

*: significant at 5% level

**: significant at 1% level

Table X.

Mean neighbourhood scores per hour and mean grooming rates in minutes per hour for trials carried out with a subgroup when a specialist was established versus when he was not.

Data		Neighbourship *) scores		Grooming **)	
Group member	Specialist	Phase		Phase	
		Control	Specialist	Control	Specialist
Ukui	Junus	3.04	5.12	1.12 min	3.60 min
Tjat	Saja	1.26	2.54	0.03 min	0.50 min
Rini	Saja	0.98	3.00	0.13 min	0.58 min
Djalan	Sakri	0.42	0.95	0.03 min	0.77 min
Djalan	Mayun	0.21	1.91	0.0 min	1.02 min
Toko	Mayun	0.05	1.03	0.0 min	0.44 min

*) maximal score per hour: 13

**) maximal rate per hour: 60 min

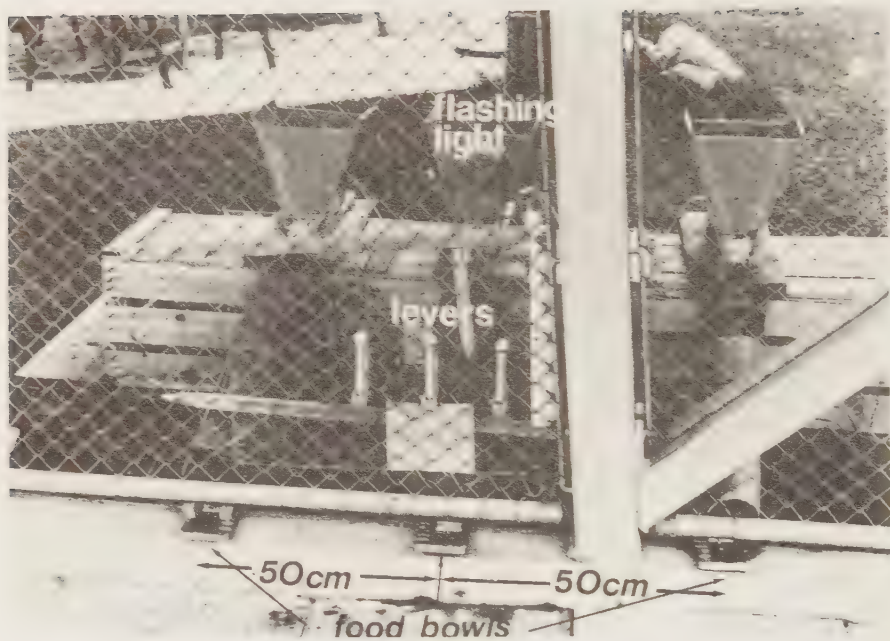


Fig. 1.: Apparatus

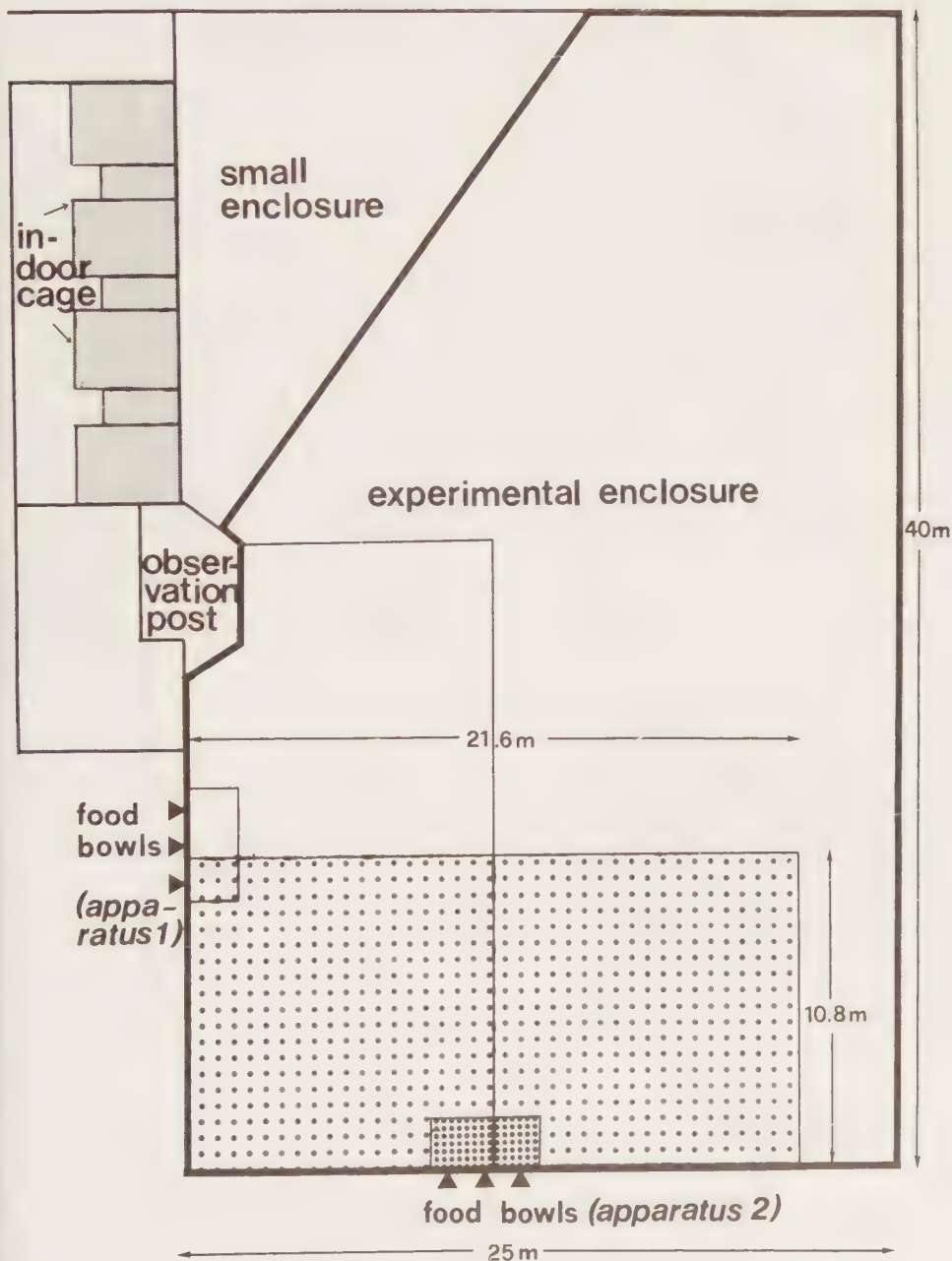


Fig. 2.: Outdoor enclosure. The subdivision into the three areas is marked for 1 apparatus site only. Area 1 (food site) is tightly dotted, area 2 is sparsely dotted. Area 3, consisting of the rest of the experimental enclosure, is left white.

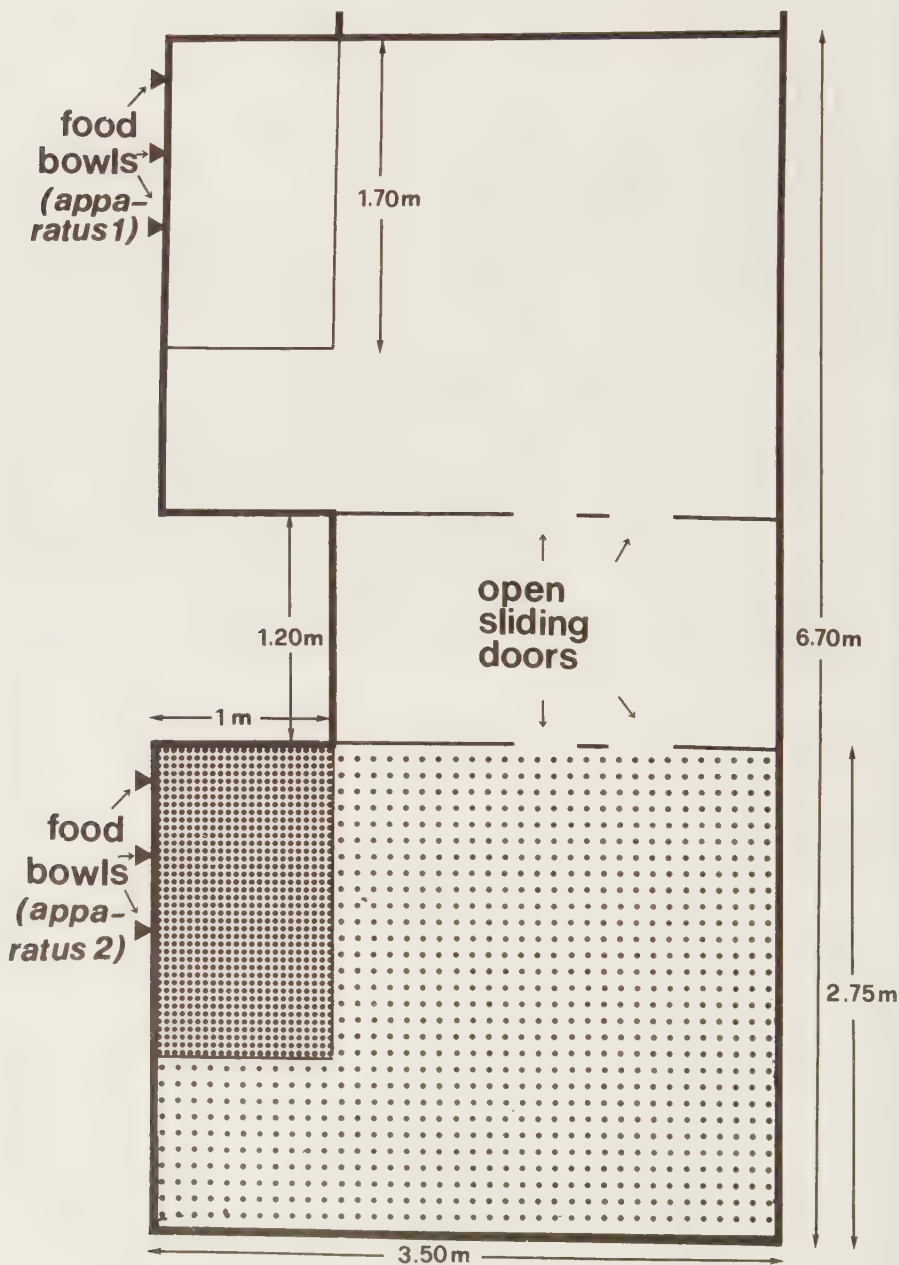


Fig. 3.: Half of indoor enclosure. The subdivision into the three areas is marked for 1 apparatus site only. Area 1 (food site) is tightly dotted, area 2 is sparsely dotted. Area 3, consisting of the rest of the experimental enclosure, is left white.

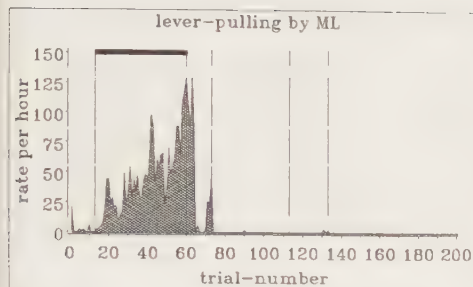


Fig. 4 a

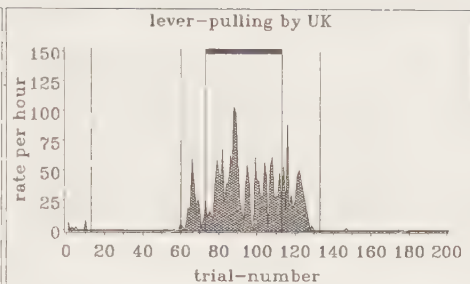


Fig. 4 b

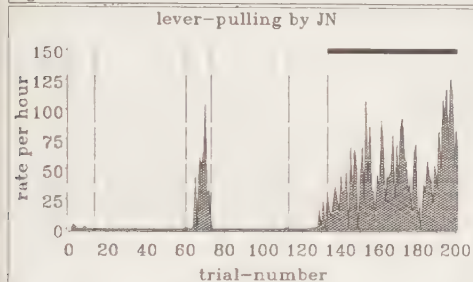


Fig. 4 c

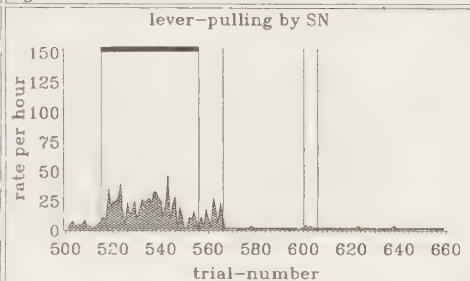


Fig. 4 d

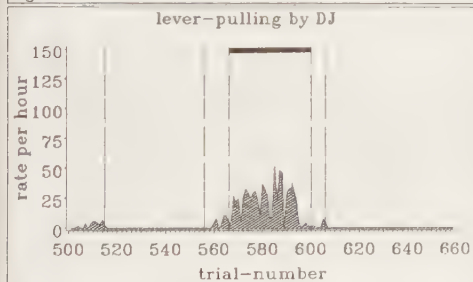


Fig. 4 e

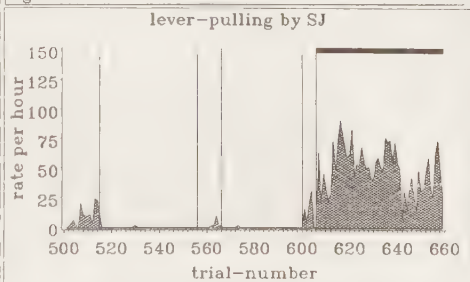


Fig. 4 f

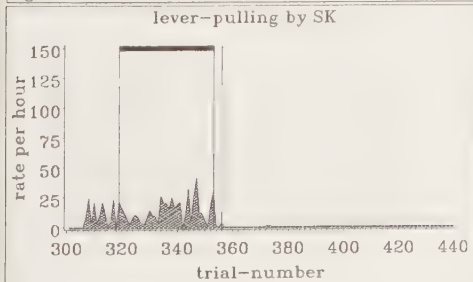


Fig. 4 g

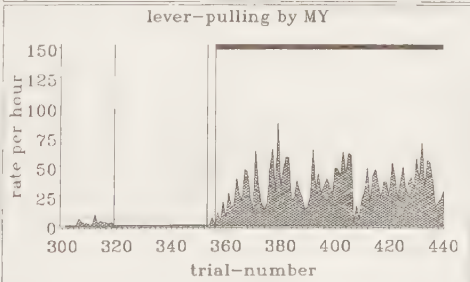


Fig. 4 h

Fig. 4.: Rates of lever pulling per trial for the 8 specialists. Vertical lines indicate the beginning or the end of a replicate. A black horizontal bar indicates the specialist's replicate.

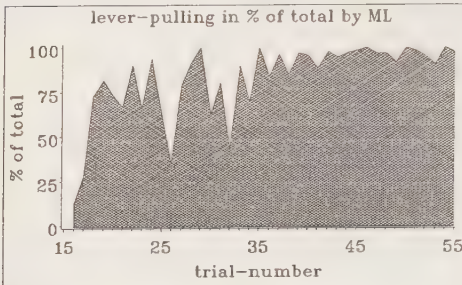


Fig. 5 a

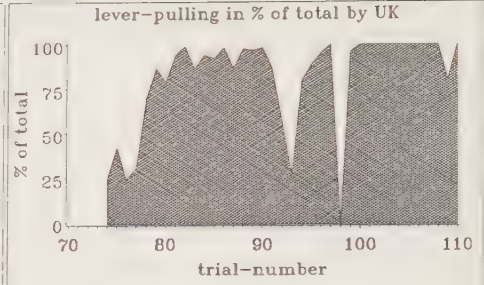


Fig. 5 b

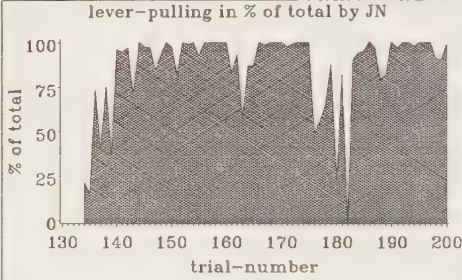


Fig. 5 c

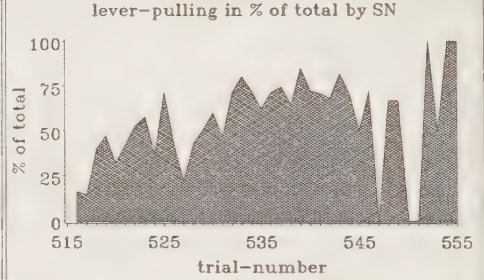


Fig. 5 d

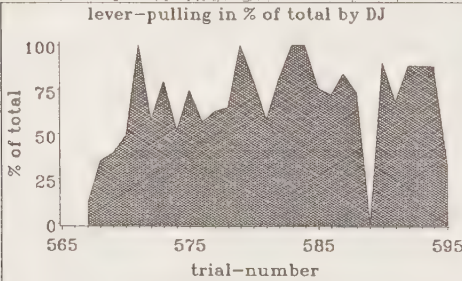


Fig. 5 e

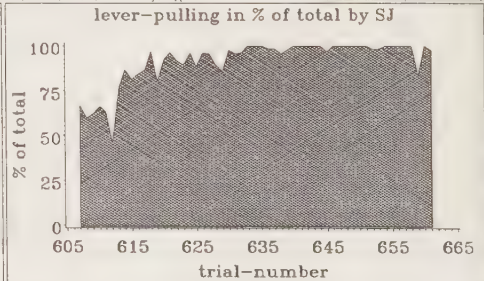


Fig. 5 f

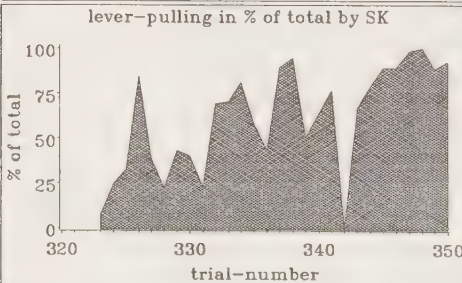


Fig. 5 g

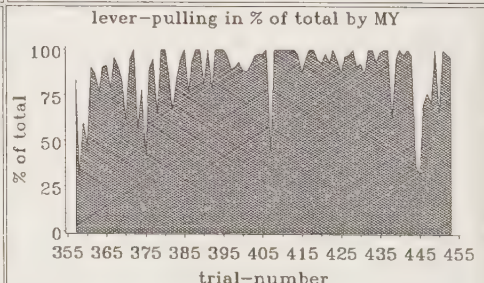


Fig. 5 h

Fig. 5.: % of total lever pulling performed by the specialist in each trial of his replicate. All zero values indicate trials in which no lever pullings occurred at all.

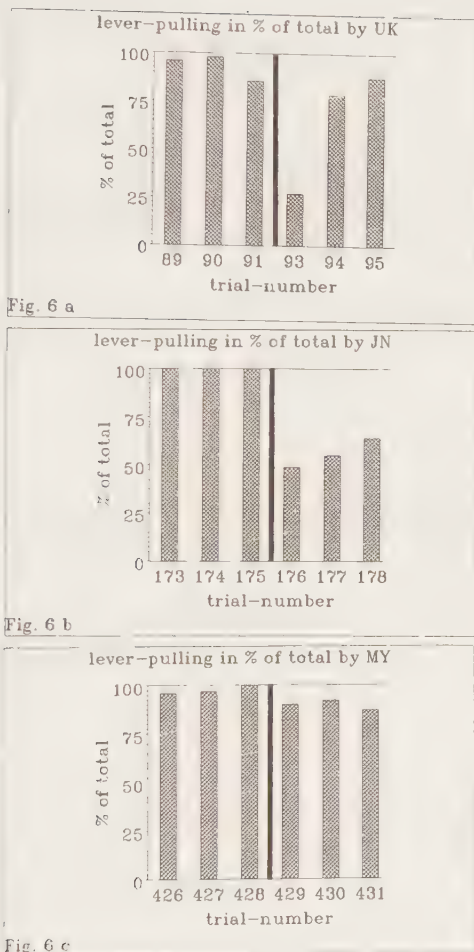


Fig. 6.: % of total lever pulling performed by the specialist in 3 trials before and 3 trials after the transfer of the experiments from the outdoor enclosure to the indoor cage or vice versa happened. Vertical bars indicate the moment of transfer.

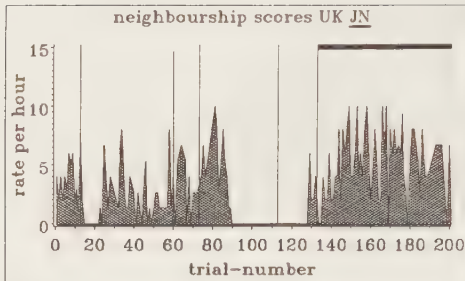


Fig. 7 a

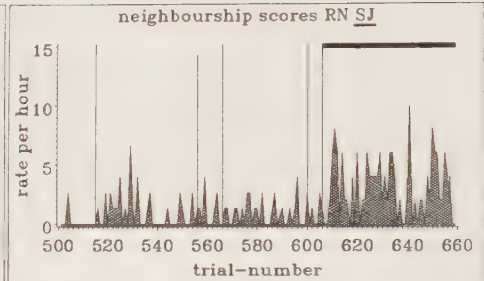


Fig. 7 b

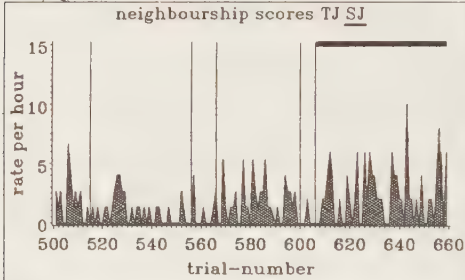


Fig. 7 c

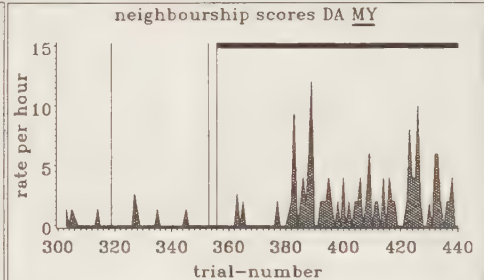


Fig. 7 d

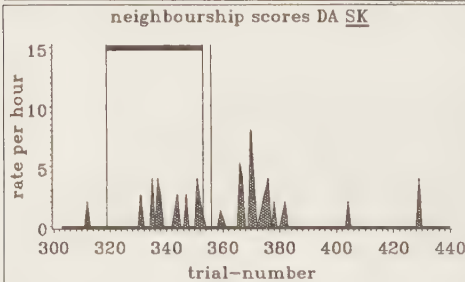


Fig. 7 e

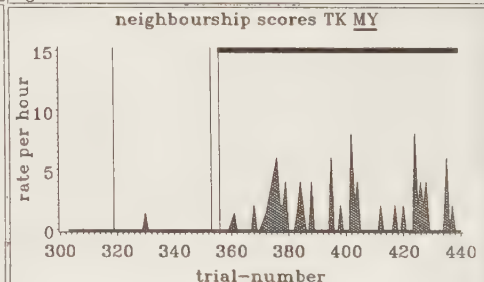


Fig. 7 f

Fig. 7.: Neighbourship scores in each trial as observed in the dyads where significant changes in social interactions happened in reaction to the experimental conditions. Vertical lines indicate the beginning or the end of a replicate. A black horizontal bar indicates the specialist's replicate. Names of specialists are underlined. No data are available for Uk-Jn for trials 15 to 20 and 90 to 128.

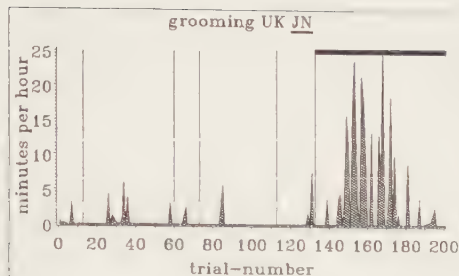


Fig. 8 a

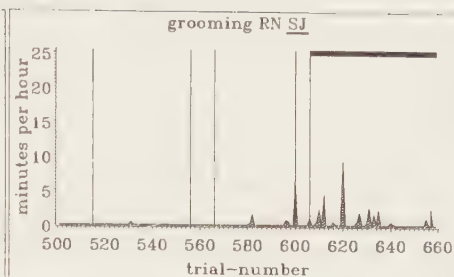


Fig. 8 b

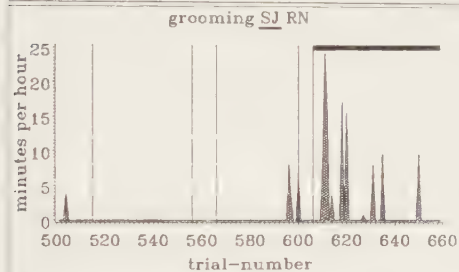


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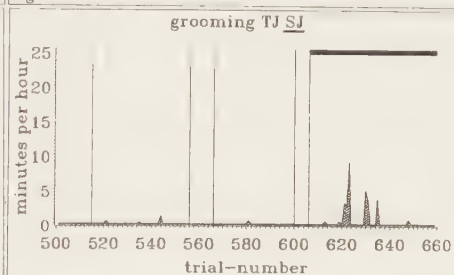


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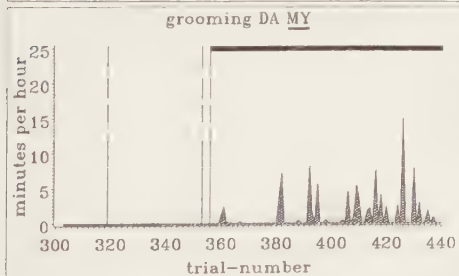


Fig. 8 e

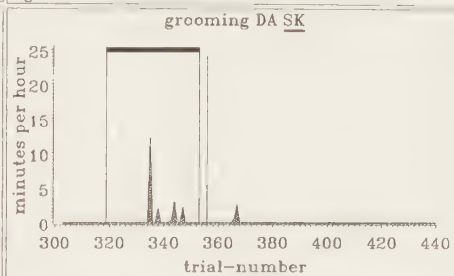


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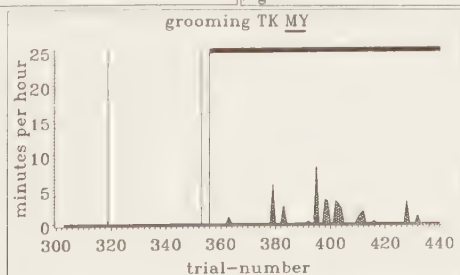


Fig. 8 g

Fig. 8.: Grooming rates per hour given to the specialist in each trial as observed in the dyads where significant changes in social interactions happened in reaction to the experimental conditions. Vertical lines indicate the beginning or the end of a replicate. A black horizontal bar indicates the specialist's replicate. Names of specialists are underlined. No data are available for Uk-Jn for trials 15 to 20 and 90 to 128.

Lebenslauf

Ich, Eduard Hermann Stambach, Bürger von Zürich, wurde am 18. Juni 1951 in Zürich geboren. Von 1958 bis 1964 besuchte ich die Primar-, von 1964 bis 1967 die Sekundarschule in Zürich. 1967 trat ich in die kantonale Oberrealschule Zürich, das heutige mathematisch-naturwissenschaftliche Gymnasium, ein, wo ich 1971 das eidgenössische Maturitätszeugnis des Typus C erlangte. 1972 immatrikulierte ich mich, mit Hauptfach Zoologie, an der Universität Zürich, wo ich 1977 mit dem Diplom als Naturwissenschaftler abschloss. Die Diplomarbeit entstand unter der Leitung von Prof. H. Kummer.

Von 1977 bis 1986 arbeitete ich als wissenschaftlicher Mitarbeiter und Assistent an der Abteilung für Ethologie und Wildforschung des Zoologischen Institutes der Universität Zürich, wo ich auch 1983 unter der Leitung von Prof. H. Kummer mit der Ausarbeitung der Dissertation beginnen konnte. Die Dissertation wurde 1987 abgeschlossen. Seit Mai 1987 bin ich als wissenschaftlicher Beamter der Eidgenössischen Versuchsanstalt für landwirtschaftlichen Pflanzenbau Zürich Reckenholz tätig.

Im Laufe meiner Studien besuchte ich Vorlesungen, Praktika, Kurse und Uebungen der Professoren, Dozenten und Lehrbeauftragten R. Bachofen, G. Bächli, E. Batschelet, J. Biegert, N. Bischof, H. Burla, P.S. Chen, C. Claude, C.D.K. Cook, P. Endress, C.H. Eugster, R. Furrer, H. Hediger, H. Heimgartner, H.R. Hohl, R. Hunsperger, E. Jungen-Hauschteck, St. Kubik, E. Kuhn-Schnyder, H. Kummer, B. Nievergelt, R. Nötiger, H.R. Oswald, D. Rast, H. Rieber, O. Rohweder, H.J. Schächli, W. Scheffrahn, J. Schlittler, H. Schmid, B. Stüssi, P. Tardent, D.C. Turner, H. Wanner, R. Wehner, O. Woodtli und V. Ziswiler.

